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# REVISION OF THE VENOMOUS SNAKES OF BOLIVIA: PART 1. THE CORALSNAKES (ELAPIDAE: *MICRURUS*)

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## ABSTRACT

Ten species of coralsnakes are known from Bolivia, and the ranges of an additional four approach Bolivia's northeastern border. Ranges of several species are expanded to accommodate recently collected material. Coralsnakes with characteristics thought to be diagnostic of *Micrurus tricolor* do not occur in Bolivia, and this species is considered to be a junior synonym of *Micrurus pyrrhocryptus*. *Micrurus frontifasciatus* is returned to the synonymy of *M. lemniscatus*. Some specimens previously referred to *M. frontifasciatus* are described as the new species *Micrurus serranus*, which is apparently restricted to dry intermontane valleys of the Andes above 1200 m. Putative subspecies of *M. spixii* occur in sympatry within Bolivia and differ from one another by a suite of morphological characters. Accordingly, we recognize *M. spixii* and *M. obscurus* as distinct species. Characteristics used to define *M. s. princeps* appear to be clinal, and this taxon is considered to be synonymous with *M. obscurus*. *Micrurus corallinus*, *M. ibiboboca*, and *M. tschudii* do not occur in Bolivia, despite earlier reports to the contrary. Claims that melanism increases with age in some species are not supported by our observations.

KEY WORDS: Bolivia, *Micrurus*, systematics

## INTRODUCTION

In 1989, Campbell and Lamar observed that, "biologically, Bolivia is very poorly known, and the distributions of dangerously venomous snakes within this country are not well understood" (p. 78). Their book, *The Venomous Reptiles of Latin America,* was a seminal publication in Neotropical herpetology and stimulated extensive research in the systematics of Neotropical pitvipers and coralsnakes. In anticipation of the second edition of this book, we began a review of Bolivia's coralsnakes.

Until recently, scientific collecting in Bolivia has been sporadic, and Bolivia's coralsnakes have never been reviewed comprehensively. Nonetheless, Bolivia contains three endemic coralsnakes, and one of these, *Micrurus diana*, was described as recently as 1983 (Roze, 1983). With the exception of *M. frontifasciatus*, Schmidt and Roze have reviewed the Bolivian species throughout their ranges in South America and Jorge da Silva and Sites have reviewed the members of the *M. frontalis* complex. These studies contained few or no Bolivian specimens, and the authors were led to a few erroneous conclusions because of limited samples.

In the 1990s, Bolivian herpetology underwent a renaissance as several groups of European, American, and Bolivian herpetologists began systematically survey-

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ing the reptiles and amphibians throughout the country. During this period, Bolivian museums amassed substantial holdings of several rare coralsnakes. Our report draws heavily on this new material.

## MATERIALS AND METHODS

In the accounts, a dash is used for ranges, whereas a slash (/) is used to separate counts from opposite sides of the same specimen. Wherever ranges appear, they are followed by means ± standard deviation. Specimens were frequently damaged, and we follow each range or character frequency with the sample size.

Except for CBF (Colección Boliviana de Fauna, La Paz, Bolivia) and NK (Museo de Historia Natural "Noel Kempff Mercado," Santa Cruz, Bolivia), institutional abbreviations are as listed in Leviton et al. (1985). Our synonymies are abbreviated in the sense that they only include references consulted during the preparation of this manuscript. Where identifications may have been in doubt, we verified actual specimens on which the citations are based.

For this study, we examined characters used in recent phylogenetic and taxonomic reviews of New World Elapidae. We routinely scored characters known to vary in some species (supralabial-prefrontal contact, supralabial number, supralabials entering orbit, temporal number, postocular number, and infralabial number) and features (frontal width, supraocular width, anal divided or entire) thought to be autapomorphies in a few species, such as an entire anal plate in *Micrurus hemprichii* and a narrow frontal in *M. surinamensis*.

We counted the number of infralabials contacting the chinshields and the number of gulars in a straight line from the last chinshield (two in coralsnakes) to the first preventral. Our definitions of preventrals and ventrals are consistent with the methodology of Dowling (1951). Therefore, our ventral counts cannot be directly compared to those of Schmidt, who routinely included number of gulars and preventrals in his ventral counts. A pair of postanal scales was included in subcaudal counts if the two sides were in contact or fused medially. We noted the number and location of entire and divided subcaudals.

We measured snout-vent length and tail length with a string and meter stick to the nearest 1 mm. Dial calipers or an ocular micrometer were used to measure head length (from the posterior margin of the last supralabial to the center of the rostral), greatest eye diameter, eye-nostril distance (from the anterior corner of the eye to the center of the nostril), greatest frontal width, and greatest supraocular width.

Among coralsnakes, pattern characteristics are particularly effective for diagnosing species. Except for *Micrurus annellatus* and *M. narduccii*, all Bolivian coralsnakes possess a tricolored triad pattern (Savage and Slowinski, 1992). We counted the number of triads on the body and tail, scoring incomplete triads at the distal end of the tail as thirds. Relative sizes of rings were quantified by counting vertebrals (i.e., the eighth row of dorsals) in the median triad. We did not measure ring lengths because number of vertebrals and ring length are redundant representations of the same character and because rings could not be easily measured on tightly coiled or twisted museum specimens. In all coralsnakes examined, individual triads were symmetrical with respect to ring length (see also Jorge da Silva and Sites, 1999). Consequently, we counted vertebrals in the red ring preceding the median triad, the median triad's first black and white or yellow rings, and the middle black ring. Distance to the first triad was expressed by counting the number of vertebrals from the parietals to the first black ring on the body. Cephalic color (when not faded) and pattern were noted for each species. Amount of black pigmentation on the chin was scored as absent, diffuse, moderate, or heavy.

## TAXONOMIC ACCOUNTS

### Elapidae

### Genus *Micrurus* Wagler, 1824

*Definition.*—*Micrurus* contains small (less than 700 mm) to large (up to 1.5 m), mostly secretive snakes with a pair of proteroglyphous fangs on the anterior end of the maxilla (Kardong, 1980) and with maxillary teeth absent behind the fang (Schmidt, 1928). The posterior part of the venom gland is inflected ventrally beneath the main body of the gland (Savitzky, 1978). The eye is relatively small and the pupil round or subelliptical. In all species, the snout is round in dorsal and lateral view, and the body is long relative to its width. The tail accounts for 4–20% of total length (Roze, 1996, provides a table of tail length/total length for most species of coralsnakes). With few exceptions, coralsnakes possess a dorsal color pattern consisting of red, yellow or white, and black rings (Savage and Slowinski, 1992).

Several authors (*inter alia*, Roze, 1996; Jorge da Silva and Sites, 1999; Slowinski, 1995) have called attention to the remarkably conservative arrangement of cephalic scales in coralsnakes. On the dorsal surface of the head, there are nine large supracephalic plates: two internasals, two prefrontals, two supraoculars, one frontal, and two parietals. Usually, one preocular, two postoculars, seven supralabials, and seven infralabials are present. A loreal scale is absent. Supralabials three and four enter the orbit except in *M. surinamensis*, where only supralabial four (rarely, only supralabial three) enters the orbit. The postoculars are followed by 0+1, 1+1, or 1+2 temporals. Relatively few gulars and preventrals separate two pairs of chinshields from the ventrals. Fifteen dorsals (17 in a few species) do not reduce in number anterior to the single (in *Micrurus hemprichii*) or divided anal plate. The subcaudals are usually divided; however, the first few (up to about the twelfth) are commonly entire in some species.

Boulenger assigned considerable taxonomic weight to contact of the mental and chinshields, and he used this character to diagnose some species such as *Elaps simonsi* (=*Micrurus pyrrhocryptus*) and *E. mentalis* (=*Micrurus mipartitus*). Similarly, this trait was used to distinguish *M. helleri* from *M. lemniscatus* (Schmidt, 1928). Fixation (or, at least, near fixation) of this trait is an apomorphy uniting the species sometimes referred to *Leptomicrurus*, and the trait occurs at low frequencies in several other coralsnakes (Amaral, 1926*b*; also see account for *M. serranus*, below). A similar case of polymorphism exists in some *Apostolepis* (Harvey, 1999).

The hemipenis is symmetrical, bilobed, noncapitate, and spinose. The *sulcus spermaticus* bifurcates proximal to the division of the lobes and extends centripetally along the lobes to the apices. A basal pocket bound medially and laterally by parallel folds is present on the asulcate side. The spines are largest near the base, diminishing in size distally. Terminal, spinelike awns are present in some species.

*Content.*—Phylogenetic analyses of coralsnakes have utilized morphology (Roze and Bernal-Carlo, 1987) and combined morphology, allozymes, and nuecleotides (Slowinski, 1995; Jorge da Silva and Sites, 2001). The results of Roze and Bernal-Carlo (1987) are difficult to evaluate because neither their characters nor their methodology are described except generally. Slowinski (1995) used clearly defined methods and recovered seemingly monophyletic clades of monadal and triadal coralsnakes. In his hypothesis, *Leptomicrurus* is nested within *Micrurus* as a basal lineage of the triadal clade. *Micrurus mipartitus* is sister to the monadal coralsnakes. Some species of Central and South American coralsnakes with a triad pattern appear to belong to the monadal clade; however, the species of this clade share a long tail and hemipenis. With the exception of *M. surinamensis*, the species of the "triadal" clade have short tails comprising 4.0–10.8% of total length in males, and species of the "monadal" clade have long tails comprising 10.0–18.5% of total length in males (Roze, 1996, his table 2). *Micruroides* (6.8–9.1% in males), *Leptomicrurus* (5.5–7.3% in males), and the *M. mipartitus* group (6.5–10.2% in males) also have short tails.

Romano (1972) synonymized *Leptomicrurus* with *Micrurus*. Although her conclusions were accepted initially by some authors (Roze, 1983; Campbell and Lamar, 1989), the genus is often recognized (Roze and Bernal-Carlo, 1987; Roze, 1996; Jorge da Silva and Sites, 2001). Here, *Leptomicrurus* is considered synonymous with *Micrurus*, because it is nested within the latter genus in Slowinski's (1995) phylogenetic hypothesis. Nonetheless, the three species commonly referred to this genus (*collaris, narduccii, scutiventris*) form a monophyletic group within *Micrurus* supported by at least two apomorphies: fixation of mental-chinshield contact (Schmidt, 1937) and strong inflection of the postero-ventral process of the venom gland (Slowinski, 1995; Roze and Bernal-Carlo, 1987; Savitzky, 1978).

Since the genus was last reviewed (Roze, 1996), Jorge da Silva and Sites (1999) partitioned the *Micrurus frontalis* complex and Campbell (2000) described a new species from Puebla, Mexico. Compelling evidence (Jorge da Silva and Sites, 2001) suggests that several taxa, notably *M. lemniscatus*, require further revision and the number of species is expected to increase. Including taxonomic changes made herein, *Micrurus* is one of the largest genera of Neotropical snakes and now includes 69 species: *M. albicinctus* Amaral, *M. alleni* (Schmidt), *M. altirostris* (Cope), *M. ancoralis* (Jan), *M. annellatus* (Peters), *M. averyi* Schmidt, *M. baliocoryphus* (Cope), *M. bernadi* (Cope), *M. bocourti* (Jan), *M. bogerti* Roze, *M. brasiliensis* Roze, *M. browni* Schmidt and Smith, *M. catamayensis* Roze, *M. circinalis* (Duméril, Bibron, and Duméril), *M. clarki* Schmidt, *M. collaris* (Schlegel), *M. corallinus* (Merrem), *M. decoratus* (Jan), *M. diana* Roze, *M. diastema* (Duméril, Bibron, and Duméril), *M. dissoleucus* (Cope), *M. distans* (Kennicott), *M. dumerilii* (Jan), *M. elegans* (Jan), *M. ephippifer* (Cope), *M. filiformis* (Günther), *M. frontalis* (Duméril, Bibron, and Duméril), *M. fulvius* (Linnaeus), *M. hemprichii* (Jan), *M. hippocrepis* (Peters), *M. ibiboboca* (Merrem), *M. isozonus* (Cope), *M. langsdorffi* Wagler, *M. laticollaris* (Peters), *M. latifasciatus* Schmidt, *M. lemniscatus* (Linnaeus), *M. limbatus* Fraser, *M. margaritiferus* Roze, *M. medemi* Roze, *M. meridensis* Roze, *M. mertensi* Schmidt, *M. mipartitus* (Duméril, Bibron, and Duméril), *M. multifasciatus* (Jan), *M. multiscutatus* Rendahl and Vestergren, *M. narduccii* (Jan), *M. nebularis* Roze, *M. nigrocinctus* (Girard), *M. obscurus* (Jan), *M. ornatissimus* (Jan), *M. pachecogili* Campbell, *M. paraensis* Cunha and Nascimento, *M. peruvianus* Schmidt, *M. petersi* Roze, *M. proximans* Smith and Chrapliwy, *M. psyches* (Daudin), *M. putumayensis* Lancini, *M. pyrrhocryptus* (Cope), *M. remotus* Roze, *M. ruatanus* (Günther), *M. sangilensis* Nicéforo-María, *M. scutiventris* (Cope), *M. serranus* Harvey, Aparicio, and Gonzales, *M. spixii*

Wagler, *M. spurrelli* (Boulenger), *M. steindachneri* (Werner), *M. stewarti* Barbour and Amaral, *M. stuarti* Roze, *M. surinamensis* (Cuvier), *M. tschudii* (Jan).

## KEY TO THE CORALSNAKES OF BOLIVIA

Coralsnakes have a remarkably conservative morphology, and characters of coloration are the most effective for identification of many species. In the key below, each couplet contains more than one character so that aberrant specimens can still be identified. In the diagnoses, characters are presented in a numbered and standardized format. We have arranged the characters so that they decrease in utility; i.e., the first few characters are more obvious and less prone to intraspecific variation than the last characters.

1. Dorsal pattern bicolored or tricolored, but rings not arranged in triads; tail long, more than 12% of snout-vent length in males . . . . . . . . . . . . . . . . . . . . . *Micrurus annellatus*
1′. Dorsal pattern of tricolored triads or dorsum black with yellow or orange ventrolateral spots; tail short, less than 12% of snout-vent length in males . . . . . . . . . . . . . . . . . . 2

2 (1′). Dorsum black except for an orange (pale yellow in preservative) frontoparietal band; circular orange or yellow spots on venter; ventrals more than 260 in both sexes; mental contacting chinshields . . . . . . . . . . . . . . . . . . . . . . . . . . . *Micrurus narducii narduccii*
2′. Dorsal pattern of triads with or without frontoparietal band; ventrals almost always fewer than 260 (rarely more than 260 in *M. lemniscatus*); mental rarely contacting chinshields or contacting chinshields at low frequencies (e.g., in 5% of *M. serranus*) . . . . . . . . . . 3

3 (2′). Anal plate entire; dorsal pattern consisting of long black rings separated by short orange or white rings; dorsal surface of head black to level of parietals (orange); ventrals 156–191 (Campbell and Lamar, 1989) . . . . . . . . . . . . . . . . . . . . . . . . . *Micrurus hemprichii*
3′. Anal plate divided or entire anal plate occurring at low frequencies (e.g., in 10% of *M. serranus*); rings on either side of middle black ring white or yellow, black rings usually shorter than red rings but may be more than five times as long as red rings in some specimens; ventrals more than 200 except in *Micrurus surinamensis* . . . . . . . . . . . . . 4

4 (3′). One supralabial (usually the fourth) entering orbit; scales of head red, edged in black; ventrals fewer than 190 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .*Micrurus surinamensis*
4′. Two supralabials (usually 3 and 4) entering orbit; dorsal surface of head black, red, or yellow, but if lightly pigmented then heavily blotched with black or with black bands; ventrals more than 200 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

5 (4′). First triad incomplete, one or two black rings on neck (in some specimens with two black rings, location of "missing" ring may be visible as row of black scales lateral to parietals; some specimens from Colombia have complete ring overlapping parietal) . . . . 6
5′. First triad complete, separated from parietal tips by 1–12 red vertebrals . . . . . . . . . . . 7

6 (5). First triad consisting of two black rings, the first greatly attenuated anteriorly and dorsally; scales of snout yellow with black blotches and margins, scales of parietal region red with black markings; black ocular band extending from supralabials 3–4 across supraoculars and frontal; exterior black rings usually shorter or incomplete ventrally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Micrurus obscurus*
6′. First triad consisting of one black ring with a near vertical anterior edge; dorsal head scales black with red margins; exterior black rings as long as white yellow rings or longest ventrally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Micrurus spixii*

7 (5′). White band crossing snout (except in rare, apparently aberrant specimens); specimens from Bolivian lowlands and humid Andean foothills also with white rings longest ventrally and usually some infralabials entirely black; specimens from dry Andean valleys also having first triad separated from parietals by 1–5 scales and parietals partially red . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8
7′. Dorsal head scales black, edged in white or white with black edges but distinct white band across snout absent; white rings longest dorsally, often restricted ventrally; pigmentation of chin variable, but anterior infralabials not entirely black; first triad more than five dorsals behind parietals or first triad contacting parietal tips . . . . . . . . . . . . 9

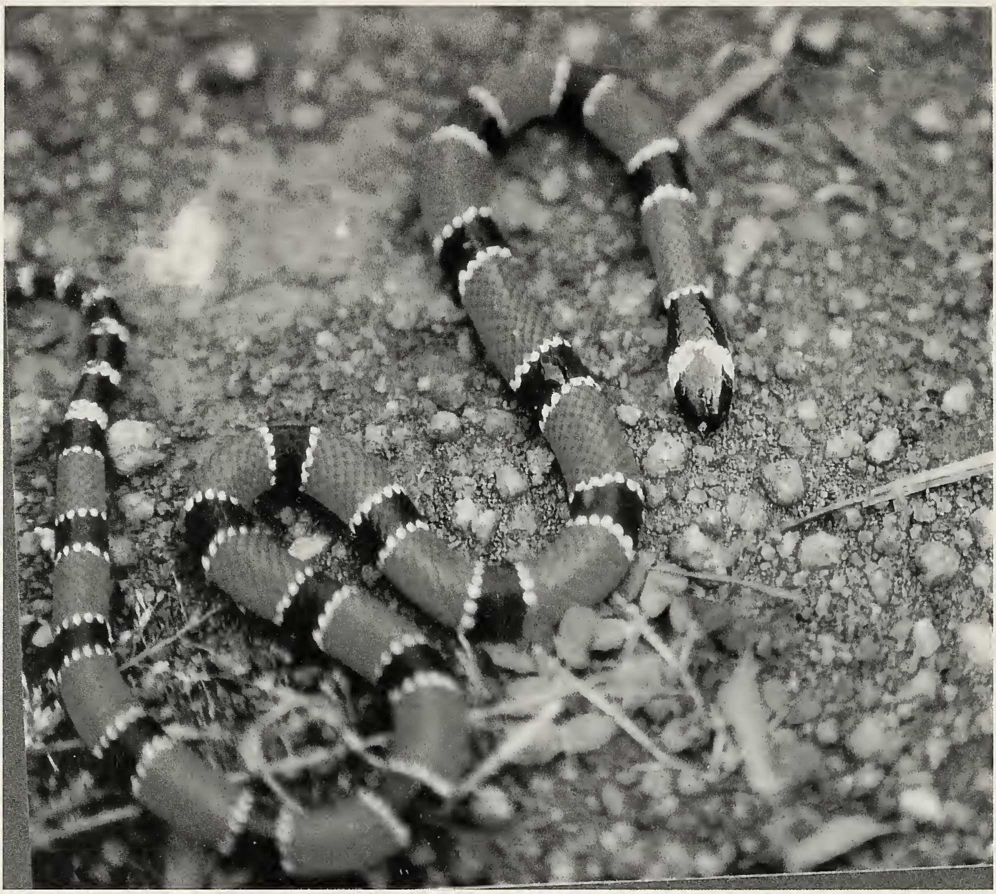

Fig. 1.—*Micrurus annellatus* from Bella Vista, Itenez province, Beni. Photo by J. Padial.

8 (7). White rings longest and immaculate ventrally; edges of scales within white snout band uniformly white, not edged in black; snout bluntly rounded; eastern lowlands and mesic Andean foothills . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Micrurus lemniscatus*

8′. White rings longest dorsally, constricted or interrupted by black rings ventrally; scales within white snout band edged in black; snout subacuminate; xeric, intermontane valleys of the Andes . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Micrurus serranus*

9 (7′). First triad contacting or closely approximating parietals; scales of red rings immaculate or with weak black edges, black pigment in red rings considerably less than in white rings; some scales in white rings with heavy black apices, giving the impression of black blotches within white rings . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Micrurus diana*

9′. Five or more red vertebrals separating first triad from parietals; scales of red rings with heavy black apices, at least posteriorly; considerably less black pigment in white rings than in red rings . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Micrurus pyrrhocryptus*

## *Micrurus annellatus* (Peters)
## (Fig. 1)

*Elaps annellatus* Peters, 1871:402. HOLOTYPE male, "Pozuzu" =Pozuzo, Peru (ZMB 7185). Boulenger, 1896:418; Peracca, 1897*a*:7.

*Elaps balzani* Boulenger, 1898*a*:130. HOLOTYPE male, "Province Yungas, at an altitude of 1600 meters" (MSNG 28874 fide Capocaccia, 1961). [The specimen came from the vicinity of Coroico (in present day La Paz department, Nor Yungas province) or Chulumani (La Paz, Sud Yungas) (Boulenger, 1898*a*, p. 128)].

*Elaps regularis* Boulenger, 1902*b*:402. HOLOTYPE female, "Chulumani, Bolivia, 2000 m" (BMNH 1946.1.17.22).

*Micrurus corallinus corallinus* (Merrem): Amaral, 1925:23 (in part); Amaral, 1926*a*:23 (in part); Amaral, 1930*a*:51–52 (in part); Fugler, 1986:57.

*Micrurus langsdorffii* Wagler: Schmidt, 1936:191 (in part); Schmidt and Walker, 1943:293.

*Micrurus balzani* (Boulenger): Schmidt, 1936:192; Schmidt and Walker, 1943:293.

*Micrurus annellatus* (Peters): Hoge and Romano, 1973:121; Duellman, 1979:456; Fugler, 1986:56; Fugler and Cabot, 1995:60.

*Micrurus annellatus annellatus* (Peters): Schmidt, 1954:323; Peters, 1960:530; Roze, 1967:6; Roze, 1970:202; Miyata, 1982:18; Roze, 1983:315; Carrillo de Espinoza, 1983:27; Campbell and Lamar, 1989:97; Golay et al., 1993:157; Carrillo de Espinoza and Icochea, 1995:19; David and Ineich, 1999:132.

*Micrurus annellatus montanus* Schmidt, 1954:322. HOLOTYPE male, "Camp 4, about 10 km. north of Santo Domingo Mine, Puno, Peru, at about 2000 m. altitude" (FMNH 40221). Roze, 1967:8; Carrillo de Espinoza, 1983:28.

*Micrurus annellatus bolivianus* Roze, 1967:7, figure 2. HOLOTYPE female, "Charobamba River, about 50 kilometers northeast of Zudañez, Chuquisaca, Bolivia" (ZMH 2706e). Roze, 1970:203; Hoge and Romano, 1973:121; Roze 1983:316; Campbell and Lamar, 1989:97; Golay et al., 1993: 158; David and Ineich, 1999:132.

*Micrurus annellatus balzani* (Boulenger): Roze, 1967:6; Roze, 1970:203; Roze 1983:315; Campbell and Lamar, 1989:97; Golay et al., 1993:157; Carrillo de Espinoza and Icochea, 1995:19; David and Ineich, 1999:132.

*Diagnosis.*—(1) Dorsal pattern tricolored or bicolored but not consisting of triads; (2) hemipenis and tail relatively long; tail length 16.1–18.3% of snout-vent length in males; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) dorsal surface of head black except for strongly angled, yellow band crossing parietal tips, temporals, and posterior supralabials (5–6 and part of 7); (7) chin pigmentation variable.

*Description.*—(Based on 5 male, 1 female, and 1 unsexed juvenile museum specimens and photographs of an unsexed specimen from Beni). Although our sample is relatively small, the material exhibits noteworthy variation in several features and largely consists of specimens not available to earlier revisors of this species. Specimens we examined range from 185–545 mm in total length and are considerably shorter than the longest previously measured specimen, a female from southern Peru that was 728 mm (Schmidt, 1954). Sexual dimorphism is evident in body proportions and counts of ventrals and subcaudals. The tail is 16.1–18.3% (16.8 ± 1.0, 4) as long as snout-vent length in males and 12.4% as long in the female specimen. Males have 187–199 (194 ± 5, 4) ventrals and 38–45 (42 ± 3, 4) subcaudals compared to 211 and 34 in the female. In NK 2047, the first three subcaudals are entire; all are divided in the other specimens. In all specimens, the anal is divided.

The head of males accounts for 2.1–2.4% (2.3 ± 0.1, 3) of snout-vent length. Eye-nostril distance is 20.3–24.2% (21.7 ± 2.1, 3) and eye diameter is 13.6–15.2% (14.4 ± 0.8, 3) of head length in both sexes. All of our specimens have 7/7 supralabials, 3–4 entering the orbit; temporals are 1+1/1+1; the prefrontal does not contact the supralabials. Five of six specimens (83%) have 2/2 postoculars; CBF 490 has 1/1 postoculars. The prefrontals do not contact the supralabials, and the supraoculars are 52–86% (66 ± 15, 4) as wide as the frontal. All specimens have 7/7 infralabials, the first pair separating the mental from the chinshields and the first four pairs contacting the first pair of chinshields. The chinshields are separated from the ventrals by three gulars and preventrals.

The dorsal surface and sides of the head are usually uniformly black except for the yellow nuchal ring. CBF 1586 possesses a circular yellow spot on the posterior edge of each supraocular. The yellow nuchal ring is longest on the sides of the head where it overlaps the temporals and supralabials 5–6 and part of 7. It shortens at the parietal tips where it overlaps the first vertebral and the posterior one to two-thirds of the parietals. In some specimens (NK 2047 and AMNH 2975), the mental and first three infralabials are black and the nuchal ring continues onto infralabials 4–5. The other specimens lack a uniformly black chin; rather, their mentals and anterior infralabials are yellow with moderate black pigment along the edges.

In our small sample, we did not observe increasing melanism with age; although the amount of black in the red rings varied from heavy (e.g., CBF 490, SVL 397 mm) to faint (photographed specimen and NK 2047, SVL 467 mm). The red coloration was completely obscured by black in the smallest specimen (AMNH 2975, SVL 330 mm) and clearly visible in the largest specimens (NK 2047, SVL 467 mm). Males have 20–25 (23 ± 2, 4) black rings on the body and 6–8 (7 ± 1, 4) black rings on the tail. The female specimen has 50 black and melanic (?) red rings on the body and 6 black rings on the tail. The red rings are as long or longer than the black rings; at midbody, the red ring is 3–6 (4 ± 1, 5), the black ring 2–4.5 (3 ± 1, 5), and the yellow ring 1–0.5 vertebrals long. Except for the nuchal rings, the body and tail rings are not strongly angled. In FML 1045, the first five black rings on the body and the rings on the tail are complete; however, the other black body rings extend only as far as the paraventrals.

Slowinski (1995) reported a hemipenis extending only 4 subcaudals in USNM 193814 and questioned whether the specimen was anomalous considering that most species in the group had hemipenes extending 8–17 subcaudals. He seems to have been correct: in NK 2047, the hemipenis extends for 20 subcaudals and bifurcates at the level of the 10th subcaudal.

*Distribution and Comparative Material.*—As currently defined, this species ranges from the Cononaco River, Ecuador (Schmidt, 1954) to Chuquisaca, Bolivia (Roze, 1967). In Bolivia, specimens occur in the Andes and adjacent lowlands of La Paz, Pando, and Beni (Fig. 2). This species was included in the Colombian fauna by Amaral (1931), who did not cite a specimen upon which his record was based. Pérez-Santos and Moreno (1988) report this species from Leticia, Amazonas, Colombia, but no museum specimens are known from there (W. W. Lamar, personal communication).

**BOLIVIA. BENI. Iténez:** Bella Vista (photo only, Fig. 1). **Unknown:** (AMNH 2975–76, Paratypes of *M. annellatus montanus*). **COCHABAMBA. Carrasco:** 30 km N Monte Punco, Yungas de Totoras, Río Yanimayo (FML 1045). **LA PAZ. Iturralde:** Yariapo (CBF 1586). **Nor Yungas:** Cotapata (CBF 1932). **Sud Yungas:** Irupana (CBF 490), "Tulimane" = Chulumani, 1800 m (USNM 98890). **PANDO. Frederico Román:** "80 km de Cachuela Esperanza" (NK 2047). **UNKNOWN:** "Sierras de Bolivia" (FMNH 22588).

*Remarks.*—Some authors have suspected that variation in length of the pale parietal band (Roze, 1983) and presence or absence of red rings were partially attributable to ontogeny (Roze, 1983; Schmidt, 1954). Roze (1983) claimed that all specimens from the Peruvian Amazon up to 1000 m and two specimens from Beni (AMNH 2975–76) were white and black. Tricolored specimens were only known from higher elevations (Schmidt, 1954; Roze, 1983) where some adults from Peru and Bolivia retain the tricolor pattern. Without explanation, Roze

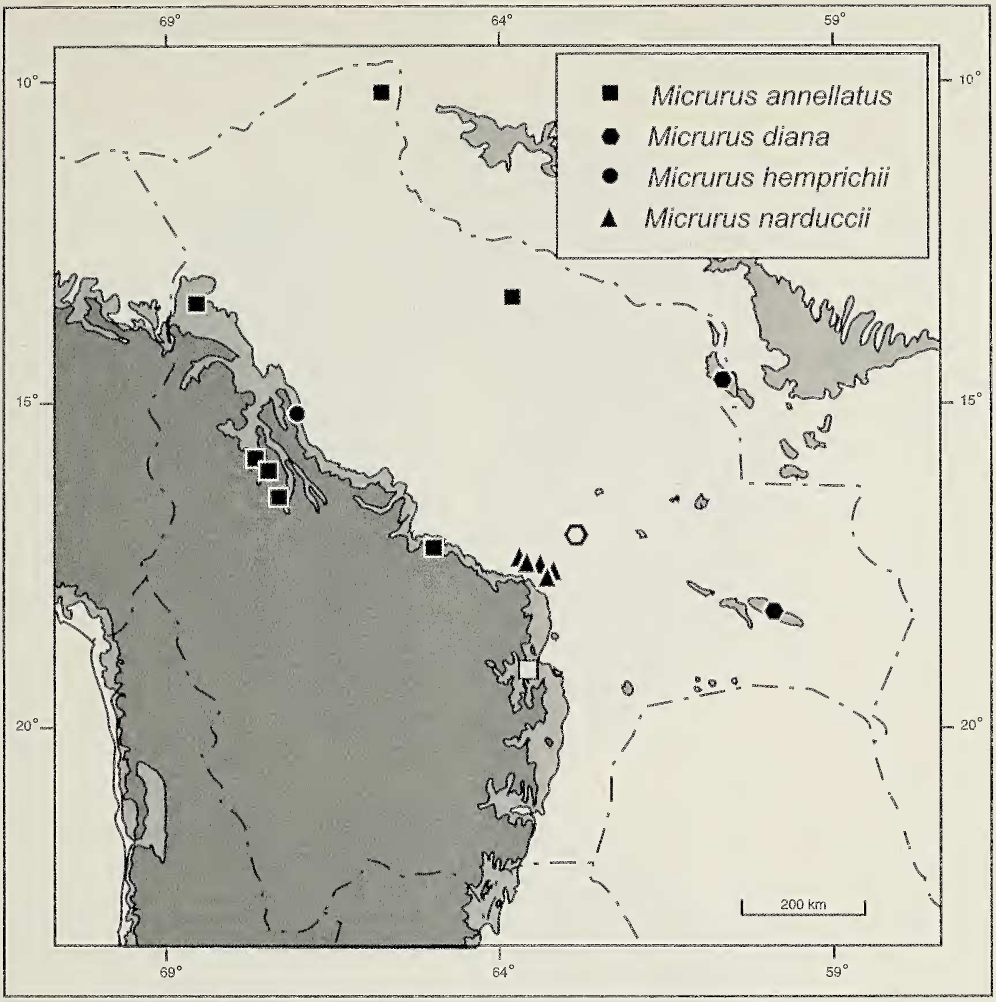

Fig. 2.—Distribution of four species of Bolivian coralsnakes.

(1983) considered ZMH 5396 from San Carlos, Beni, to be an intergrade between the subspecies *balzani* and *annellatus*.

The large adult (SVL 476 mm) from the lowlands of Pando and the specimen illustrated in figure 1 from Beni both have red rings, contradicting claims that presence of red is correlated with ontogeny or elevation. Length of the pale parietal band shows little variation in Bolivian samples and does not appear to vary with age.

A strong case for recognizing subspecies of *Micrurus annellatus* has not been made. Roze (1996) recognizes three subspecies and separates them using number of postoculars, presence of red rings, and length of postocular ring. Using his key, CBF 490 is the only specimen with one postocular and keys to *M. annellatus balzani*. The remaining specimens key to *M. a. annellatus* because they have two postoculars and their parietals are one- to two-thirds black. Thus, if the two subspecies are valid, they occur in the same cloud forests along the slopes of the

Andes in La Paz and Cochabamba. It is unlikely that subspecies maintain their identity in sympatry, and we believe that number of postoculars is polymorphic within a single, monotypic species.

### *Micrurus diana* (Roze)
(Fig. 3)

*Micrurus frontalis diana* Roze, 1983:324. HOLOTYPE male, "vicinity of Santiago, Provincia Chiquitos" Santa Cruz, Bolivia, 700 m (FMNH 159889). Campbell and Lamar, 1989:115; Golay et al., 1993:167.

*Micrurus diana* (Roze): Roze, 1994:179; Roze, 1996:152; Harvey, 1998:151, 353; Jorge da Silva and Sites, 1999:170; David and Ineich, 1999:136.

*Diagnosis.*—(1) Dorsal pattern of white, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) first triad complete; (7) first triad contacting parietal tips; (8) parietals black with white edging; scales of snout either white with black edging or black with white edging (see remarks below); (9) scales of white rings edged in black and white rings with irregular black blotches; red rings nearly or completely immaculate; (10) white rings longest dorsally, constricted or broken ventrally by black rings; (11) chin mostly immaculate, red or red and white; (12) 9–11 triads on the body; (13) relative lengths of rings variable.

*Remarks and Variation.*—This species was described relatively recently (Roze, 1983) and a detailed redescription was provided by Jorge da Silva and Sites (1999). Since we do not have access to new material, we will only comment on some discrepancies between Jorge da Silva and Sites' (1999) diagnosis and the specimens we examined.

NK 219 and AMNH 120600 were also examined by Jorge da Silva and Sites (1999), but NK 219, in particular, violates key parts of their diagnosis of this species: (1) The dorsal snout scales (rostral, nasal, preocular, prefrontals, frontal) of NK 219 are black with white edges rather than white with black edges. Just the opposite is true for the other specimens. (2) In NK 219, the chin is red rather than white. White pigment is clearly present on the chinshields in the type specimens. (3) The white rings are shorter (2 vertebrals in the middle triad in NK 219) or as long as the middle black ring and shorter than the exterior black rings. Sites and Jorge da Silva (1999) characterize this species as having white rings longer than the black rings. In NK 219 and AMNH 120600, the black exterior rings are 4–4.67 vertebrals long and noticeably longer than the middle ring (3 vertebrals in both specimens). (4) Including the nuchal triad, AMNH 120600 (a male) and FMNH 195899 (a female) both have 9 body triads (including the triad on the neck, Fig. 3), rather than 10–11 (Jorge da Silva and Sites, 1999). To us, the differences between topotypic material and the specimen from Velasco Province are considerable, and the status of the population in the Parque Noel Kempff Mercado should be reconsidered when more material becomes available.

*Micrurus diana* may be synonymous with *Micrurus brasiliensis*. We tentatively recognize these species because their known distributions are distantly allopatric. Reference to their key and point-by-point comparisons of their diagnoses indicate that Jorge da Silva and Sites (1999) considered these species to be distinct on the basis of one character. *Micrurus diana* has more extensive black pigmentation on its parietal scales: black with white margins versus anterior and medial parts of parietals black in *M. brasiliensis*. *Micrurus diana* is known from only a few

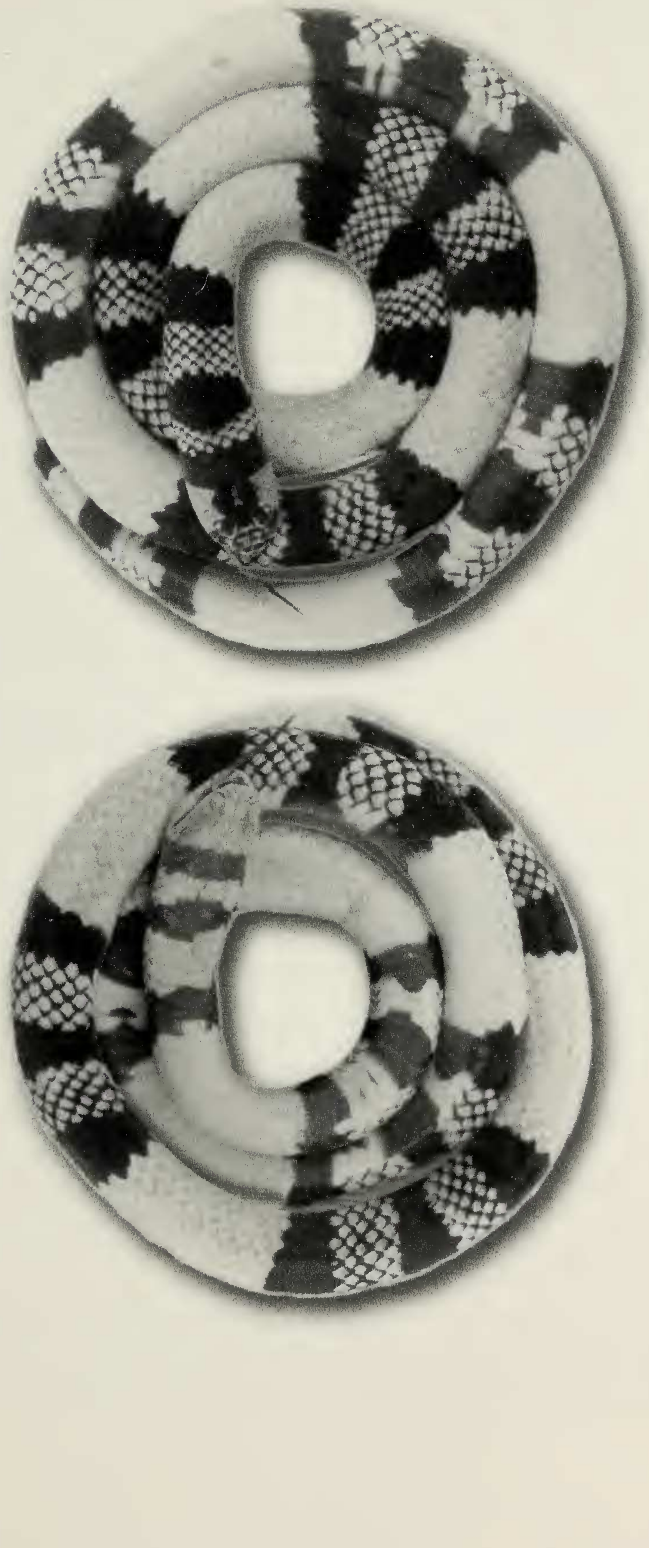

Fig. 3.—*Micrurus diana*, paratype (AMNH 120600 M, SVL 536 mm) from the vicinity of Santiago, Chiquitos, Santa Cruz.

specimens. On the other hand, *Micrurus serranus* may be closely related to the *M. frontalis* complex, and the amount of pigmentation on its parietals is highly variable. We do not place much confidence in this supposed difference between *M. brasiliensis* and *M. diana*. The morphometric analysis does not reveal differences between these species. Figure 2 in Jorge da Silva and Sites (1999) shows that the ranges and means of canonical variables 1 and 2 for *M. diana* are almost completely encompassed by the wider ranges for *M. brasiliensis*. Ranges for selected meristic and morphometric data tabulated in tables 1 and 2 of Jorge da Silva and Sites' publication overlap for these species. In both species, the first triad contacts the parietals in some or all specimens.

To published accounts (Roze, 1983; Jorge da Silva and Sites, 1999), we would add that the prefrontal does not contact the supralabials, and the first four infralabials contact the first pair of chinshields. The number of entire anterior subcaudals is variable in this species. The first ten are entire in NK 219 and the first 12 are entire in AMNH 120600, whereas all of the subcaudals are divided in FMNH 195899.

*Distribution and Natural History.*—Harvey (1998) identified NK 219 and reported this species for the first time from the Serranía de Huanchaca (Fig. 2); it was previously known only from the type locality. Roze (1983) observed that *Micrurus pyrrhocryptus* occurred on adjacent mountains and in the intervening lowlands. He suspected that *M. diana* might be restricted to the Serranía de Santiago. The Serranía de Santiago and the Serranía de Huanchaca are remnants of the Brazilian Shield and are ecologically very similar (Killeen and Schulenberg, 1998). Roze's (1983) characterization of the type locality as an " 'island' surrounded by swampy lowlands" certainly applies to both localities during the rainy season.

Jorge da Silva and Sites (1999) report a personal communication from P. Bettella, who sent them a slide of a specimen taken from San Ramón (provincia Ñuflo de Chávez), Santa Cruz, Bolivia. We have not examined the slide and have not been unable to locate the specimen in the Museo Noel Kempff Mercado, where P. Bettella deposited most specimens he collected.

**BOLIVIA. SANTA CRUZ. Velasco:** Serranía de Huanchaca (NK 219). **Chiquitos:** "surroundings of Santiago, 700 m," (AMNH 120600, FMNH 195864, FMNH 195899, paratypes).

## *Micrurus hemprichii* (Jan)

*Elaps hemprichii* Jan, 1858:523. COTYPES sex unknown, Colombia (MSNM, destroyed in World War II) and an unknown locality (NHMW, status unknown) [Schmidt (1953*a*) doubts that one of the types could have come from Colombia and proposes "vicinity of Bartica, British Guiana" as the new type locality. However, Roze (1955) argues that the original type locality may have been correct, and he reports a specimen from only a few kilometers of the Colombian border in Venezuela]. Boulenger, 1896:421; Boulenger, 1898*a*:131.

*Micrurus hemprichii* (Jan): Amaral, 1925:17; Amaral, 1930*c*:230; Amaral, 1948*b*:158; Hoogmoed, 1979:277; Fugler, 1986:57; Vanzolini, 1986:24; Fugler and Cabot, 1995:60.

*Micrurus hemprichi hemprichi* (Jan): Schmidt, 1953*a*:166; Golay et al., 1993:170.

*Micrurus hemprichii hemprichii* (Jan): Roze, 1955:481; Brongersma, 1967:73; Roze, 1970:210; Hoge and Romano, 1972:108; Hoge and Romano, 1973:125; Cunha and Nascimento, 1982:13; Nascimento et al., 1987:57; Campbell and Lamar, 1989:118; Jorge da Silva, 1993:71; David and Ineich, 1999:141.

*Micrurus hemprichi ortoni* Schmidt, 1953*a*:166. HOLOTYPE male, "Pebas, Peru" (MCZ 12423). Schmidt, 1955:348; Peters, 1960:530; Golay et al., 1993:170.

*Micrurus hemprichii ortoni* Schmidt: Roze, 1967:29; Roze, 1970:210; Hoge and Romano, 1972:108; Hoge and Romano, 1973:126; Carrillo de Espinoza, 1983:31; Dixon and Soini, 1986:142; Campbell and Lamar, 1989:118; David and Ineich, 1999:141.

Boulenger (1898*a*) reported on a single specimen of *Micrurus hemprichii* collected by Balzan from "Missiones Mosetenes" (presumably in the Serranía de Mosetenes, Cochabamba, Bolivia; Fig. 2). In his review of this species, the specimen was not examined by Schmidt (1953*a*), who pointed out that the record was a "logical extension of the range along the Amazonian slopes of the Andes." We did not examine the specimen and are aware of no new Bolivian material for this species. To our knowledge, morphological data have never been reported for the Bolivian specimen. Jorge da Silva (1993) described 30 specimens from Rondônia, near Bolivia's northeastern border.

### *Micrurus lemniscatus* (Linnaeus)
(Fig. 4)

*Coluber lemniscatus* Linnaeus 1758:224. HOLOTYPE "Asia" (in error, LECTOTYPE NRS L-93, designated by Roze, 1989) [Schmidt and Walker (1943) restricted the type locality to Belém, Pará, Brazil; however, Roze (1967) thought that the specimen most likely came from the northern Guianas].

*Elaps lemniscatus* (Linnaeus): Günther, 1859:85 (part); Cope, 1859:346; Günther, 1861:15; Jan, 1863: 113a; Jan and Sordelli, 1872:42 table 5, figure 1; Cope, 1876:182; Boulenger 1896:430 (in part).

*Elaps marcgravii* (Wied-Neuwied): Boulenger, 1896:428 (part); Boulenger, 1898*a*:131; Werner, 1901: 10.

*Elaps frontifasciatus* Werner, 1927:250. HOLOTYPE male, "Bolivia" (NHMW 18298).

*Micrurus lemniscatus* (Linnaeus): Beebe, 1919:216; Amaral, 1925:24; Amaral, 1926*c*:39 (in part); Schmidt 1936:201; Schmidt and Walker, 1943:294; Amaral, 1948*a*:9; Amaral, 1948*b*:158; Schmidt and Inger, 1951:464; Schmidt, 1955:349; Peters, 1960:531; Hoogmoed, 1979:277; Rivero-Blanco and Dixon, 1979:297; Fugler, 1986:57; Vanzolini, 1986:24; Nascimento et al., 1988: 55; Fugler and Cabot, 1995:60; Di-Bernardo et al., 2001:60.

*Micrurus helleri* Schmidt and Schmidt, 1925:129. HOLOTYPE male, "Pozuzo, Huanuco, Peru" (FMNH 5577). [Added to synonymy by Amaral, 1930*a*:54]

*Micrurus lemniscatus lemniscatus* (Linnaeus): Amaral, 1944:89; Burger, 1955:40; Brongersma, 1967: 73–74; Roze, 1967:32; Roze, 1970:212; Hoge and Romano, 1973; Roze, 1983:329; Cunha and Nascimento, 1982:15; Cunha et al., 1985:70; Campbell and Lamar, 1989:127; Golay et al., 1993: 173; Roze, 1996:189.

*Micrurus lemniscatus frontifasciatus* (Werner): Roze 1967:34; Roze, 1970:212; Hoge and Romano, 1973:127.

*Micrurus lemniscatus diutius* Burger 1955:8. HOLOTYPE male, "Tunapuna, Trinidad" (FMNH 34472). Roze, 1955:483; Schmidt, 1957:62; Roze, 1967:34; Roze, 1970:212; Hoge and Romano, 1973:127; Roze, 1983:329; Campbell and Lamar, 1989:128; Golay et al., 1993:174; Roze, 1996: 190; Kornacker, 1999:155.

*Micrurus lemniscatus carvalhoi* Roze, 1967:33, figure 11. HOLOTYPE male, "Catanduva, São Paulo, Brazil" (USNM 76341). Roze, 1970:212; Hoge and Romano, 1973:128; Roze, 1983:329; Campbell and Lamar, 1989:127; Roze, 1996:190.

*Micrurus lemniscatus helleri* (Schmidt and Schmidt): Roze, 1967:35; Hoge and Romano, 1973:128; Miyata, 1982:18; Roze, 1983:329; Carrillo de Espinoza, 1983:33; Dixon and Soini, 1986:143; Campbell and Lamar, 1989:128; Jorge da Silva, 1993:72; Golay et al., 1993:174; Carrillo de Espinoza and Icochea, 1995:19; Roze, 1996:191; Kornacker, 1999:156.

*Micrurus frontifasciatus* (Werner): Roze, 1983:313, 326. Campbell and Lamar, 1989:116 (in part); Golay et al., 1993:168; Roze, 1996:175 (in part); David and Ineich, 1999:140. [**revised synonymy,** see remarks]

*Micrurus ibiboboca* (Merrem): Fugler, 1986:57.

*Diagnosis.*—(1) Dorsal pattern of white, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) first triad complete; (7) 2–6 red vertebrals separating first triad from parietals; (8) dorsal surface of head black with white band crossing snout; margins of scales within white band not edged in black; parietals partly red; (9) extent of black pigment in red and white rings variable; (10) white rings longest ventrally, never constricted or broken ventrally by black rings; (11) mental and some anterior infralabials entirely black (i.e., band across snout broken by entirely black infralabials) or red; (12) 9–15 triads on the body and 1–1.67 triads on the tail in Bolivian specimens (7–17 and 0.67–2 across the species range,

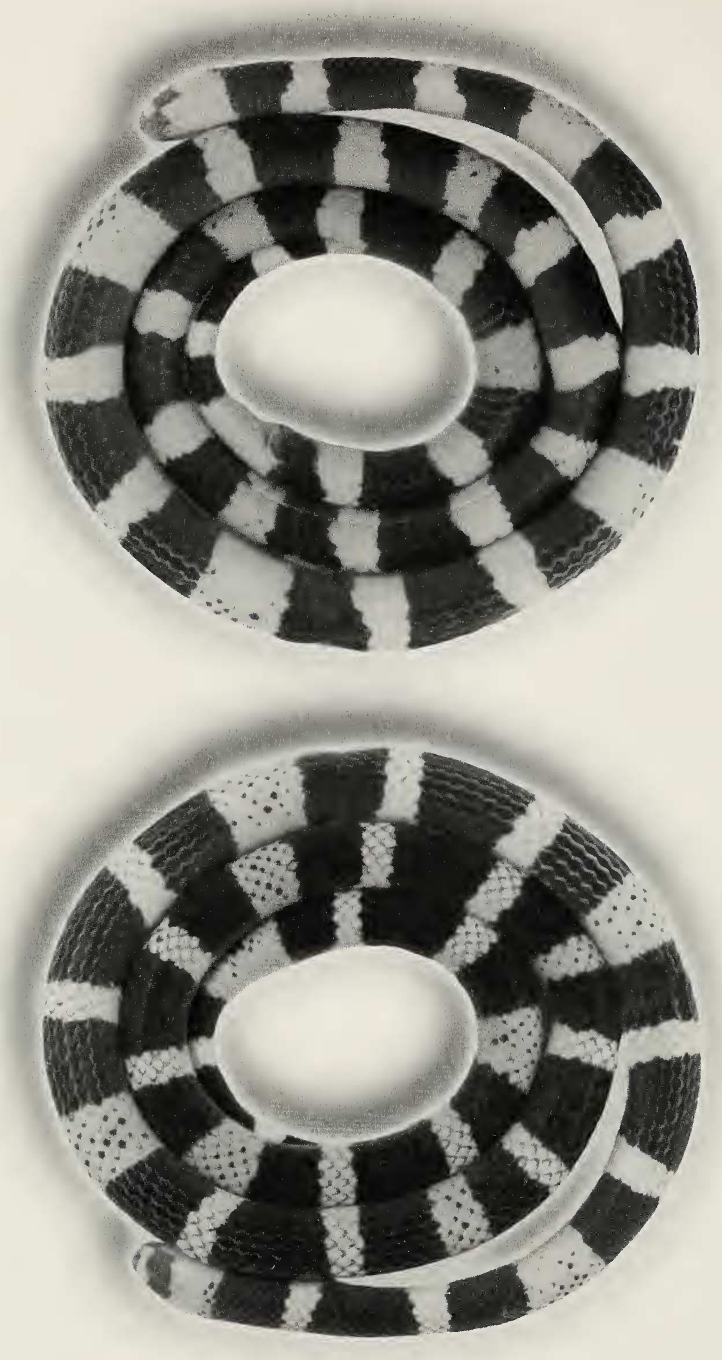

Fig. 4.—*Micrurus lemniscatus* (KU 183491 F, SVL 625 mm) from 21 km SW of Villa Tunari, Chapare, Cochabamba.

Campbell and Lamar, 1989); (13) white rings always smaller than exterior black rings in Bolivian specimens and elsewhere (Campbell and Lamar, 1989).

*Description.*—(based on 11 females, 8 males, and 6 unsexed juveniles). *Micrurus lemniscatus* is one of the most distinctive coralsnakes in Bolivia. Bolivian specimens were 244–1047 mm, the largest being a female (CBF 982). CBF 665 (also a female) with a snout-vent length of 995 mm would be the longest specimen, however most of its tail is missing. The tails of females were 6.6–10% (8.6 ± 1.0, 9) and the tails of males were 8.0–11.3% (9.2 ± 1.2, 7) as long as their snout-vent lengths. The length of the head accounts for 1.4–2.3% (1.9 ± 0.2, 9) of snout-vent length in females and 2.0–2.4% (2.2 ± 1.4, 7) in males. Eye-nostril distance is 21–24% (21 ± 1, 5) of head length. The snout of this species is more bluntly rounded than is the snout of the superficially similar *M. pyrrhocryptus* and *M. serranus* (Fig. 6).

In our sample, variation in cephalic squamation is low. In one specimen (UMMZ 56891, 4.2%, 24), the prefrontal contacts the second supralabial on both sides. A single postocular is present on both sides of two specimens (8.3%, 24). In all but one specimen (95.8%, 24), 1+1/1+1 temporals are present. In UTA 34563, the sixth supralabial contacts the parietals on both sides (0+1/0+1 temporals). Only rarely (4.2% of the time, 24), the fourth infralabial fails to contact the first pair of chinshields. The mental does not contact the chinshields. Three to five (4 ± 1, 25) gulars and preventrals separate the chinshields from 218–266 (239 ± 16, 11) ventrals in females and 210–236 (220 ± 10, 8) ventrals in males. Females have 27–38 (31 ± 3, 11) and males have 29–39 (33 ± 4, 8) subcaudals. The anal and the subcaudals are divided in most specimens. In three individuals (12.5%, 24), the first four or five subcaudals are entire.

This species is characterized by four well-defined bands (black, white, black, red) on the dorsal surface of the head. The first black band overlaps the rostral, internasals, prenasal, and first infralabial. The scales in the white band are immaculate and do not have black margins. The white band overlaps the prefrontals, the anterior edge of the frontal, and most of the postnasal, preocular, and supralabials 2–3. In one specimen (CBF 665), the white band does not reach the supralabials, the first five of which are uniformly black. The extent of the bands is somewhat variable so that the anterior one-fourth of the supraoculars may also be white in some specimens. The second and broader black band covers most of the frontal and the anterior one-third of the parietals, supraoculars, postoculars, supralabials 4–5 and part of the anterior temporals. In some specimens, the anterior edge of the sixth supralabial is also covered by this band. The parietals may be immaculate, have black apices (e.g., UMMZ 56891), or have irregular black edges and smudges (e.g., NK 968, UMMZ 67928). AMNH 110449 is unusual in having immaculate black prefrontals that restrict the white band to the sides of the head (USNM 19726 from Loreto, Peru, exhibits a similar pattern).

Banding on the head is interrupted by a distinctive chin pattern. In most specimens, the mental and first three infralabials are immaculate black and sharply contrast with the mostly white chinshields. This black infralabial pattern interrupts the white prefrontal band on the sides of the head (Fig. 6). In some specimens, the black infralabials are present on one side only (e.g., CBF 442 and 458) or absent altogether (e.g., UMMZ 57696, small black blotch present on one side; USNM 193722–23 from Huanuco, Peru, also lack black infralabials). The gulars and preventrals are usually immaculate.

Bolivian specimens of *Micrurus lemniscatus* have 9–15 (10 ± 1, 24) triads on the body and one to one and two-thirds on the tail. The first triad is separated from the parietals by 2–5.5 (3.0 ± 0.9, 23) red vertebral scales. The amount of black pigment in the red and white rings is highly variable in our sample, and we find no evidence that increased melanism is correlated with ontogeny. Some of the largest specimens (e.g., UMMZ 57696, 942 mm long; CBF 426, 749 mm) have nearly immaculate white rings, whereas several juveniles (e.g., UTA 34563, 300 mm long) have scales with black apices in nearly all of the white rings. In most specimens all of the rings on the body are complete. In UMMZ 56891, the exterior rings are broken on the flanks in triads 7–9: i.e., complete middle rings are flanked by black dorsal and ventral blotches in these triads. Ventrally, the black rings do not interrupt the white rings and the rings are almost always immaculate. In Bolivian specimens, the exterior black rings are smaller than or equal to the middle black ring (57–100%, 77 ± 13, 23), and the white rings are always smaller than the exterior black rings (20–71%, 48 ± 16, 23). In the median triad, the middle black ring was 50–233% (132 ± 50, 23) as long as the red ring.

In life (field notes of M. B. Harvey based on MBH 6129), the white band across the snout and white rings of the first two triads had a faint yellow tinge; the remaining white rings were grayish white. The red rings were Flame Scarlet (#15, Smithe, 1975).

*Natural History.*—NK 564 was found eating a swamp eel (*Synbranchus* sp.). The specimen from El Refugio was caught in August in a small mammal trap set next to a rapidly drying grassy pond in savanna, approximately 0.5 km from forest. When disturbed, the specimen hid its head under its coils, elevated its tail, and waved the underside of its tail at the observer. In addition to *Synbranchus*, this species also feeds on amphisbaenians, caecilians, small teiids, and other fish (Roze, 1983; Vanzolini, 1986). Beebe (1946) also collected this species in marshy fields adjacent to forest.

*Distribution and Comparative Material.*—In Bolivia (Fig. 5), the range of this species is more extensive than that depicted by maps published by Campbell and Lamar (1989) and Roze (1996). As for many other Amazonian species, *Micrurus lemniscatus* occurs in the humid forests of the Andean foothills as far south as Santa Cruz. The discovery of this species in the Serranía de Santiago is, at first, surprising because most of the herpetofauna in this area is Chacoan (Gans, 1960). However, stands of high tropical dry forest separate the Beni from the lower scrub-like vegetation of the Gran Chaco. The Serranía de Santiago lies in this band as does Finca Dos Milanos, and the region is inhabited by both Amazonian (e.g., *Apostolepis nigroterminata*, Harvey, 1999) and Chacoan reptiles and amphibians.

**BOLIVIA. BENI. Cercado:** El Toco, 14°53′06″S, 64°39′03″W (NK 968). **Gral. José Ballivián:** San Borja (CBF 458), Rurrenabaque (NK 1938). **Marban:** 60 km S Trinidad (NK 564). **Marmoré:** San Joaquín (FMNH 152316). **Yacuma:** Estancia "Totai" =Toataisal (NK 1958), Estancia Kamandu, 57 km E San Borja (CBF 426), Espíritu (CBF 441–42, CBF 456). **Unknown:** "Rio Itenez, Puerto Capitan Vazquez," not traced (AMNH 110449–50), "Villa Bella Rio Beni," not traced (UMMZ 57696), "along Beni River" (AMNH 22272), no other data (AMNH 2977, CBF 1450). **COCHABAMBA. Chapare:** 21 km SW Villa Tunari, 680 m (KU 183491). **LA PAZ. Larecaja:** Zona Unutuluni, 2 km del Río Tora, 250 km [southwest] del Guanay, 1200 m, (CBF 515). **Sud Yungas:** Sapecho, (CBF 1170). **PANDO. Frederico Román:** "Manao" = Nuevo Manoa, "extreme NE corner Bolivia junction of Rio Abuna with Madeira" (UMMZ 56891). **Manuripi/Madre de Dios (border):** Junction of the Río Madre de Dios and Río Sena, bank not specified (UMMZ 59772). **SANTA CRUZ. Andrés Ibáñez:** Km 14 on old road to Cochabamba (NK 513). **Chiquitos:** Finca Dos Milanos (UTA 34563), Campamento Murcielago, 59° 03 S, 18° 06′ W (NK 2247). **Ichilo:** Buena Vista (UMMZ 67928), San Carlos (NK 104), Campamento Espejo, Río Blanco, Parque Nacional Amboró (NK 2027). **Ñuflo de Chávez:** Las Trancas (NK 2028), Concepción (CBF 665). **Velasco:** Estancia El Refugio (uncatalogued, collector's tag M. B. Harvey 6129).

**ECUADOR. MORONA-SANTIAGO:** USNM 283970–71. **PASTAZA:** USNM 232437–41.

**PERU. HUANUCO:** USNM 193720–23. **LORETO:** USNM 197295–96.

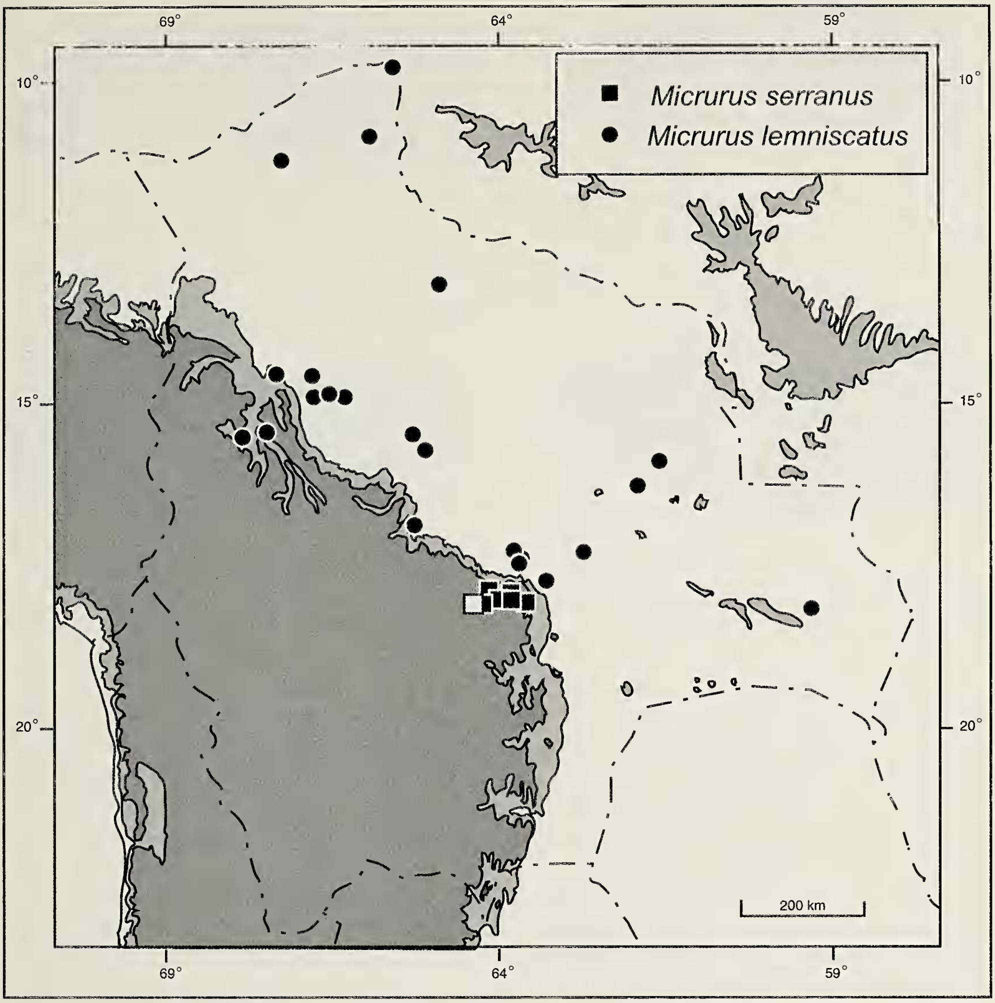

Fig. 5.—Distribution of *Micrurus lemniscatus* and *M. serranus*.

**SURINAME. SURINAME:** USNM 13823
**TRINIDAD. ST. GEORGE:** USNM 286963.

*Remarks.*—Werner (1927, page 250) described an adult male coralsnake (NHMW 18298) collected by Staudinger from "Bolivia" as *Elaps frontifasciatus*. The original description is inadequate to unequivocally identify this species. However, Heinz Grillisch of the NHMW kindly examined the specimen and answered several of our questions regarding its characteristics. From Werner's description, the holotype had a snout-vent length of 1040 mm and tail length of 75 mm. It has 1+1 temporals, 222 ventrals, a divided anal plate, and 31 divided subcaudals. The snout is black and a long black band crosses the ocular region to cover supralabials 3–5. The suture between the parietals bears a large black spot. The body has eight triads with one complete and one incomplete triad on the tail. In each triad, the middle black rings (about 8 scales long) are longer than the external ones (about 5 scales long). Finally, the white rings are as long as the external

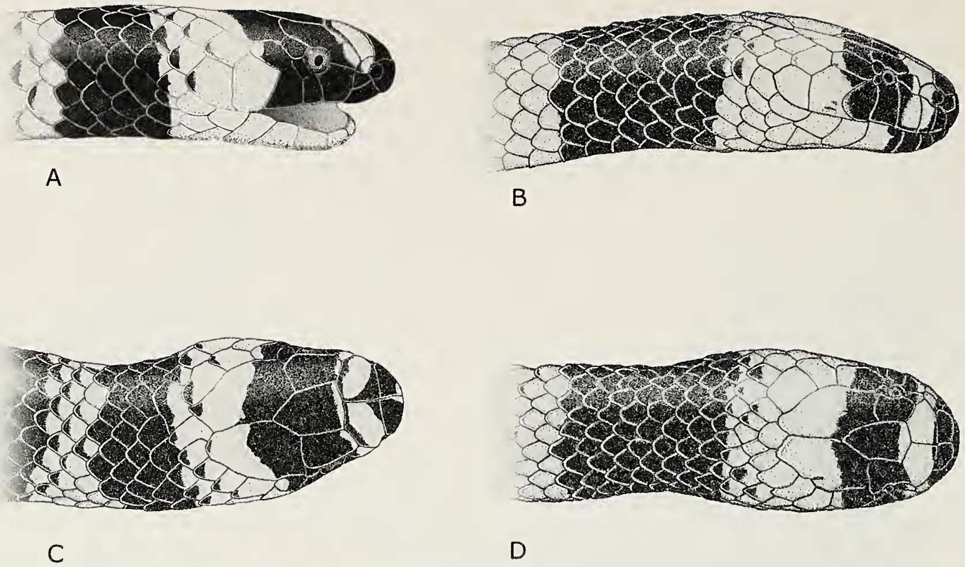

Fig. 6.—Cephalic squamation and pattern of *Micrurus serranus* (A, C, Holotype, UTA 34561 M) and *M. lemniscatus* (B, D, KU 183491).

black rings. Dr. Grillitsch further clarified that white rings are longest ventrally and all rings are immaculate ventrally. The white band across the snout encompasses part of supralabial 1 and 3 and all of 2, the preocular, the prefrontals, and the anterior edge of the frontal and supraoculars. Importantly, the scales in the white band are not edged in black. The ventral surface of the head is immaculate to the level of the first body triad.

Werner's species was correctly thought to be synonymous with *Micrurus lemniscatus* by Amaral (1930*a*). However, later authors (Campbell and Lamar, 1989; Roze, 1996) thought it was conspecific with the undescribed species (Fig. 6) we name below and known to these authors from photos from Cochabamba (Campbell and Lamar, 1989, their figure 55) and an unknown locality in Bolivia (Roze, 1996, his color figure 28). Unlike the holotype of *M. frontifasciatus* and other *M. lemniscatus* (characteristics of *M. lemniscatus* in parentheses), the scales in the prefrontal band have black edges (scales in band uniformly white), the white rings are invaded by the black rings ventrally and have prominent black blotches (white rings immaculate ventrally), and the white rings are longest dorsally and shortest ventrally (the reverse is true) in *M. serranus*. In most specimens of *M. lemniscatus* uniformly black anterior infralabials interrupt the white prefrontal band (never the case in *M. serranus*), however, like the holotype of *M. frontifasciatus*, occasional specimens of *M. lemniscatus* have immaculate chins on one (e.g., CBF 458) or both (e.g., NK 513) sides.

We were unsuccessful in our attempts to determine a more precise locality for Werner's holotype. Mr. Staudinger was an insect dealer in Dresden, Germany. Entomologists at the Zoologisches Museum in Berlin where Staudinger's neartic butterfly collection is housed were unable to confirm that Staudinger had visited Bolivia. Roze (1996) reported this species from "low and high mountain dry forest, cloud forest and lowland gallery forest on the eastern slopes of the Andes in southeastern Peru and northern Bolivia, between about 600 and 2500 m." Presumably, Roze thought the holotype came from low elevations in the Yungas of La Paz and believed it to occur at higher elevations in dry intermontane valleys based on communications with Noel Kempff Mercado, who supplied Roze's color figure 28 of *Micrurus serranus*. Roze's concept of this species is a composite of *M. lemniscatus* and *M. serranus*. The distribution he (Roze, 1996) reports for *M. frontifasciatus* is not applicable to any species of coralsnake.

*Micrurus frontifasciatus* was recently reported from Almeirim, Pará, Brazil (Guedes, 2000). This locality on the north bank of the Amazon and near the river's mouth is 1600 airline km from the known range of the exclusively montane species *M. serranus*. Not having examined the specimen, we prefer not to speculate as to its identity.

Concerns about the reality of subspecies of *M. lemniscatus* have been registered (Cunha and Nascimento, 1982; Abuys, 1987; Nascimento et al., 1988). The subspecies are defined by number of ventrals, number of body triads, and length of the white rings. When a recent key to the subspecies (Roze, 1996) was used to identify our sample, 21% of the sample keyed out to *M. l. carvalhoi* (white rings 1–1.5 dorsals long), 53% keyed out to *M. l. diutius* (ventrals fewer than 225 in males and fewer than 242 in females), and 26% keyed out to *M. l. helleri* (ventrals more than 228 in males and more than 242 in females). However, each of the specimens that keyed to *M. l. carvalhoi* has fewer than 225 ventrals if a male and fewer than 242 if a female. Thus, these specimens would be classified as *M. l. diutius* because male *M. l. carvalhoi* have 228–254 ventrals and females have 250–263 ventrals (Roze, 1996). Although most Bolivian specimens of *M. lemniscatus* key to *M. l. diutius*, this subspecies is thought to occur in northern South America not extending south of the Amazon. Bolivia is not included in published ranges of *M. l. diutius* (Campbell and Lamar, 1989; Roze, 1996). The race of *M. lemniscatus* in Bolivia has previously been referred to *M. l. helleri*. We do not believe that these observations suggest an allopatric population or wider range of *M. l. diutius*. The characters used to define these subspecies are unreliable, and the subspecies themselves may not be valid. Nonetheless, some populations currently referred to *M. lemniscatus* represent distinct evolutionary lineages (Jorge da Silva and Sites, 2001). It remains to be seen whether more careful revision of this complex will support the subspecific taxa, and their use should be abandoned in the meantime.

## *Micrurus narduccii narduccii* (Jan)
(Fig. 7)

*Elaps narduccii* Jan, 1863*b*:222. HOLOTYPE lost, "Bolivia" (CSI, number unknown; type locality restricted to "Buenavista, Provincia de Santa Cruz" =Buena Vista, Provincia Ichilo, by Roze and Bernal-Carlo, 1987). Boulenger, 1896:433; Griffin, 1916:220.

*Micrurus narduccii* (Jan): Schmidt, 1936:190 (in part); Romano, 1972:113 (in part); Campbell and Lamar, 1989:134 (in part).

*Leptomicrurus narducci* (Jan): Roze, 1967:3; Hoge and Romano, 1973:128 (in part).

*Leptomicrurus narduccii* (Jan): Schmidt, 1937:363 (in part); Hoge and Romano, 1966:5; Fugler and Cabot, 1995:60.

*Micrurus narducci* (Jan): Fugler, 1986:57.

*Leptomicrurus narduccii narduccii* (Jan): Roze and Bernal-Carlo, 1987:591; Roze, 1996:134.

*Micrurus narduccii narduccii* (Jan): David and Ineich, 1999:147.

*Diagnosis*.—(1) Dorsum black except for orange nuchal ring and, often, an orange ring around base of tail; circular orange or yellow spots on venter; (2)

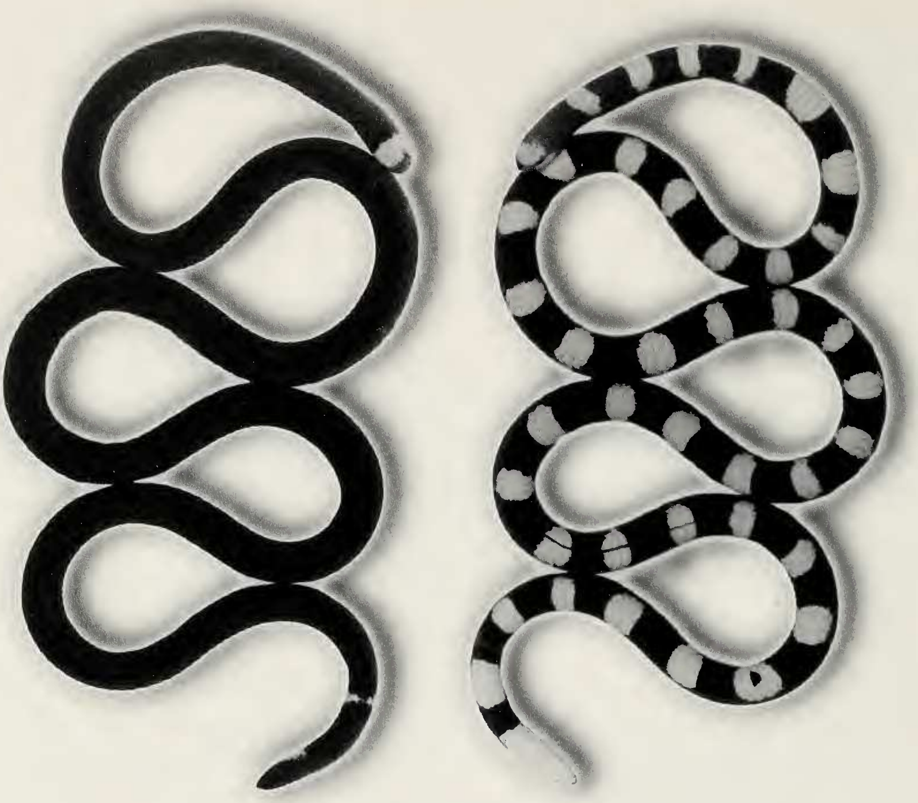

Fig. 7.—*Micrurus narduccii narduccii* (UMMZ 67891 M, SVL 462 mm) from Buena Vista, Andrés Ibáñez, Santa Cruz.

hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental broadly contacting chinshields; (5) anal scale usually divided; (6) dorsal head scales immaculate black except for orange band crossing all of frontal and anterior portions of parietals to supralabials and onto underside of head; (7) subcaudals 17–20 in females and 23–26 in males.

*Description.*—(based on 10 females and 12 males). *Micrurus narduccii* is not only the most distinctive of Bolivia's coralsnakes, but also its most sexually dimorphic. The sexes are immediately recognizeable on the basis of nonoverlapping ventral counts, subcaudal counts, and relative tail and snout-vent lengths. In our sample, females were 421–579 mm in total length, and their tails were 3.6–4.5% (4.1 ± 0.3, 9) as long as their snout-vent lengths. Males were 406–528 mm long, and their tails were 5.8–7.1% (6.7 ± 0.4, 12) as long as their snout-vent lengths. Relative to congeners, the body of this species is much more attenuate so that head length accounts for only 1.3–1.5% (1.4 ± 0.1, 8) of snout-vent length in females and 1.5–1.7 (1.6 ± 0.1, 11) in males. The diameter of the eye is comparable to other coralsnakes and is 9–14% (12 ± 1, 15) of head-length; eye-nostril distance is 20–24% (22 ± 1, 15) of head-length.

Bolivian *Micrurus narduccii* have the cephalic squamation characteristics typical of most congeners. The prefrontals do not contact the supralabials in any of our sample. Two postoculars are invariably present and usually followed by 1+1/1+1 temporals. Two specimens have 1+2 temporals on one side only, and one specimen lacks the first temporal (i.e., 0+1) on one side. The supraoculars are 67–87% (78 ± 7, 15) as wide as the frontal. Supralabials 4 and 5 are partially fused leaving a subocular on one side and are completely fused on the other side of UMMZ 63169. All other specimens have 7/7 supralabials. The mental broadly contacts the chinshields in all specimens. The first three (20% of the time, 22) or four (80%, 22) infralabials contact the first pair of chinshields, and the fourth or third and fourth contact the second pair. Four (77%, 22) or five (23%, 22) gulars and preventrals separate the chinshields from the ventrals. Females have 314–324 (318 ± 3, 10) ventrals and 17–20 (18 ± 1, 9) subcaudals, whereas males have 264–278 (274 ± 5, 12) ventrals and 23–26 (25 ± 1, 12) subcaudals. The anal plate and all subcaudals are divided.

The black snout and orange frontoparietal band are immaculate. The extent of the frontoparietal band varies somewhat: the frontal, postoculars, first temporals, and supralabials 5 and 6 are completely orange. The band covers two-thirds to three-fourths of the parietals, part of the second temporals, and most or all of the supraoculars. In some specimens the band may also overlap the posterior edge of the prefrontals, posterior edge of supralabial 3, all of 4 and the anterior edge of supralabial 7. Thus, the eye is ordinarily enclosed in the black band covering the snout, the only exception being UMMZ 67893, where the preocular and supralabial 3 are also yellow on one side only. On the ventral surface of the head, infralabials 6 and 7 and sometimes part of 5, the gulars, and the first few ventrals are black. The rest of the chin is orange.

The dorsum is immaculate black. Ventral blotches are orange (pale yellow in preservative), extend onto the paraventrals, and cover from 1.5–6 ventrals. On individual specimens, size of blotches is not constant. However, the different-sized blotches and spacing of the blotches do not seem to form any consistent pattern that might be interpreted as being derived from the triad pattern. In some specimens (e.g., UMMZ 60566), several pairs of ventral blotches are fused leaving a black spot or one black ventral in the center of each fused pair. With longer bodies, females have more blotches (44–52; 47 ± 3, 10) than males (38–44; 41 ± 2, 12).

Male specimens have 2–3 blotches on the ventral surface of the tail. Except for the first subcaudal, the ventral surface of the tail is uniformly yellow in most (67%, 10) females or two discrete blotches may be present (33%, 10). A usually complete (incomplete in UMMZ 63168) ring encircles the tail at the level of the third subcaudal in both sexes, and a second ring in the middle of the tail is broken vertebrally.

*Natural History Notes.*—Two Bolivian specimens (UMMZ 60565 and 67893) had swallowed whole *Bachia dorbignyi* head first. A third specimen (UMMZ 60568) contained a tail which appears to be from *B. dorbignyi.* The distal tip of this tail was swallowed first.

*Distribution.*—**BOLIVIA. SANTA CRUZ. Andrés Ibáñez:** Santa Cruz de la Sierra (CM 114), Espejillos (NK 489), Terevinto (NK 517), El Potrerillo (NK 2029), Buena Vista [CM 2705, 2870, 2895, MCZ 19724, UMMZ 60565–60568, UMMZ 63168, UMMZ 67891 (n = 3), UMMZ 67892, UMMZ 67893]; Río Surutú (UMMZ 63169–63170). **Sara:** unknown (CM 8).

*Remarks.*—Most references to this species are based partially or exclusively (the latter publications purposefully left out of our synonymy) on specimens of *Micrurus narduccii melanotus* (Peters). The account by Campbell and Lamar (1989) also includes data for *Micrurus scutiventris* Cope. These authors considered *Micrurus karlschmidti* Romano (replacement name for *Leptomicrurus schmidti* Hoge and Romano and a synonym of *M. scutiventris*) to be a synonym of *M. narduccii*. The subspecies of *Micrurus narduccii* appear to be allopatric, and numbers of subcaudals do not overlap between females and rarely overlap between males of the two subspecies. Our ranges for subcaudals (17–20 in females and 23–26 in males) are slightly broader than those reported by Roze (1996); female *M. n. melanotus* have 21–27 subcaudals and males have more than 24–35 (usually 28–35 based on 30 specimens, Roze, 1996). Campbell and Lamar's (1989) map does not include the range of *M. n. narduccii*, the shaded portion in the Pando region is probably based on the imprecise type locality "Bolivia." *Micrurus narduccii narduccii* is known only from the rainforests at the base of the Andes around Santa Cruz de la Sierra (Fig. 2), and recent collecting efforts elsewhere in the country have failed to discover additional populations.

### *Micrurus obscurus* (Jan), **new combination**
(Fig. 8A, 8C)

*Elaps corallinus* var. *obscura* Jan in Jan and Sordelli, 1872:41, plate 6, figure 2. HOLOTYPE (MSNM, destroyed in World War II), "Lima" in error [type locality designated as "Iquitos, Peru" by Schmidt, 1953*b*:175].

*Elaps heterozonus* Peters, 1881:52. HOLOTYPE from "Sarayacu (Ecuador)" (ZMB 9813). Boulenger, 1896:417; Barbour and Noble, 1920:619; Amaral, 1925:18.

*Elaps spixi* (Wagler): Werner, 1901:10.

*Elaps princeps* Boulenger, 1905:456. SYNTYPES "Province Sara, Department Santa Cruz de la Sierra, Bolivia" (Roze, 1989:14, designated BMNH 1946.1.20.44, a male, as a lectotype). Griffin, 1916: 220. [**new synonymy**, see remarks]

*Micrurus spixii* (Wagler): Schmidt, 1936:198 (in part); Amaral, 1948*a*:159; Vanzolini, 1986:24; Fugler, 1986:58 (in part); Fugler and Cabot, 1995:60 (in part).

*Micrurus spixii obscura* (Jan): Schmidt and Walker, 1943:294.

*Micrurus spixi obscurus* (Jan): Schmidt, 1953*b*:175; Schmidt, 1955:350; Roze, 1955:476; Peters, 1960: 532; Lancini, 1979:192; Golay et al., 1993:181.

*Micrurus spixi princeps* (Boulenger): Schmidt, 1953*b*:175; Golay et al., 1993:182.

*Micrurus spixii obscurus* (Jan): Roze, 1967:42; Roze, 1970:218; Hoge and Romano, 1973:129; Duellman, 1978:261; Miyata, 1982:18; Carrillo de Espinoza, 1983:43; Roze, 1983:335; Dixon and Soini, 1986:146; Campbell and Lamar, 1989:146; Carrillo de Espinoza and Icochea, 1995:19; Roze, 1996:216; Kornacker, 1999:159.

*Micrurus spixii princeps* (Boulenger): Roze, 1967:43; Roze, 1970:218; Roze, 1983:335; Campbell and Lamar, 1989:146; Roze, 1996:217.

*Diagnosis*.—(1) Dorsal pattern of yellow, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) first triad usually incomplete (if complete, the first black ring is very short and edges the parietals; a "remnant" of this ring is often evident as a row of black scales on the side of the neck): two black rings on neck, the first strongly angled anteriorly along midline; (7) dorsal surface of snout red, parietal region yellow; black band crossing frontal and supraoculars to supralabials; (8) apices of yellow rings with more black pigment than apices of scales in red rings; (9) yellow rings longest ventrally, some black rings greatly constricted or interrupted ventrally; (10) mental and some anterior infralabials edged in black, remaining scales of chin mostly immaculate; (11) parietals immaculate yellow or with black blotching; scales of snout moderately blotched; (12) pre-

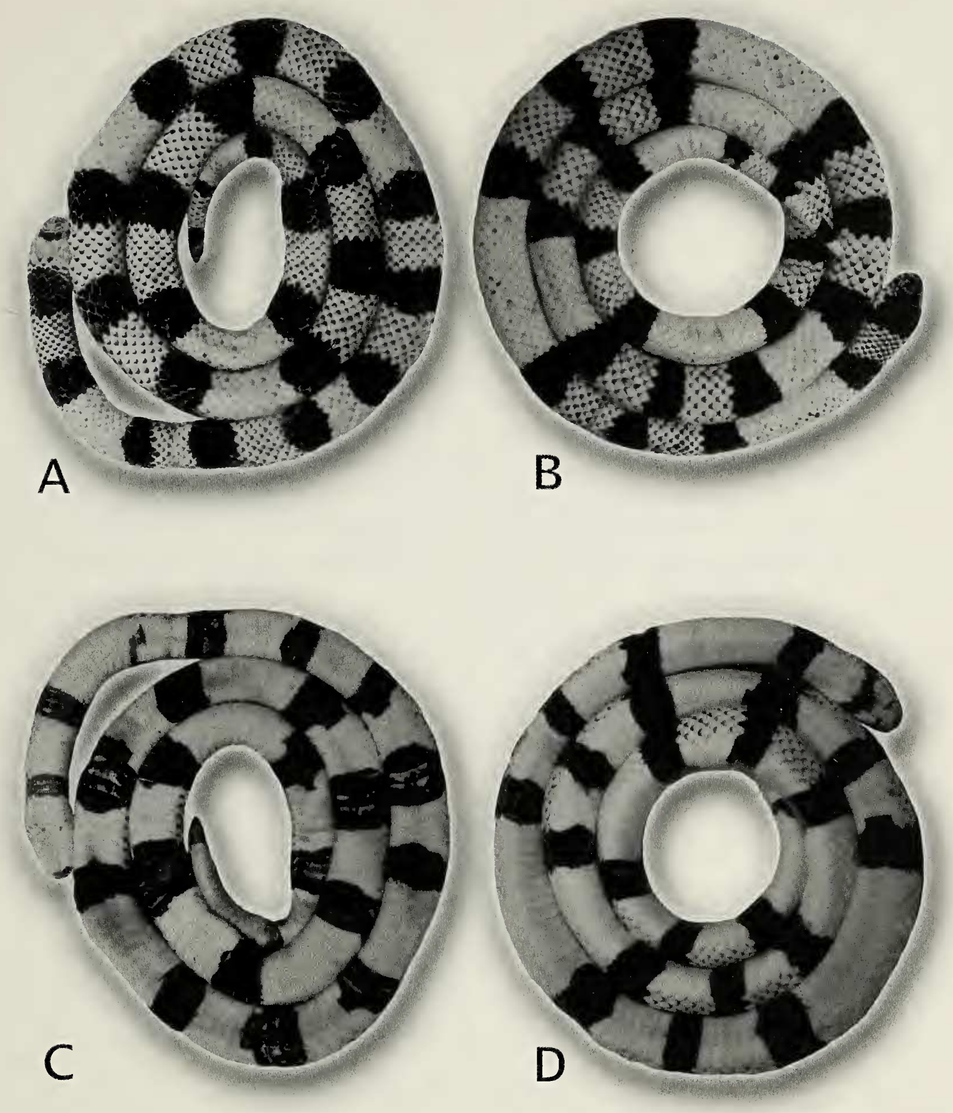

Fig. 8.—*Micrurus obscurus* (A, C; NK 158 F, SVL 1124 mm) from Parque Nacional Amboró, Ichilo, Santa Cruz, and *M. spixii* (B, D; NK 604 M, SVL 1172 mm) from the Serranía de Huanchaca, Velasco, Santa Cruz.

frontal contacting the supralabials in about 60% of the specimens; (13) 6–9 body triads (as few as 4 in specimens outside Bolivia, Roze, 1996), 0.67–1 triads on tail; (14) yellow rings longer or only slightly shorter than exterior black rings.

*Description.*—(Based on 12 males, 11 females, and 7 unsexed juveniles). This species is the largest Bolivian coralsnake. Extremes in our sample are 1345 mm (CM 126) and 1186 mm (NK 158) for the largest male and female, respectively, and 278 mm for the smallest juvenile (AMNH 122498). The tail is 5.1–6.2% (5.8 ± 0.4, 10) as long as snout-vent length in females and 5.0–7.0 (5.7 ± 0.5, 12) as long in males. Head length accounts for 2.0–3.3% (2.4 ± 0.4, 9) of snout-vent length in females and 2.0–2.5 (2.4 ± 0.3, 12) in males. The distance from the anterior border of the eye to the center of the nostril accounts for 14–22% (20 ± 2, 21) of head length.

Contact between the prefrontals and the supralabials is common in this species, occuring 60% (30) of the time. In our sample, 7/7 supralabials and 2/2 postoculars are always present; the third and fourth supralabials invariably enter the orbit. Temporals usually (67% of the time, 31) number 1+1/1+1; although about one-third of the specimens have 1+2 temporals on one or both sides (33%, 31). The supraoculars are 64–92% (73 ± 8, 22) as wide as the frontal.

Seven infralabials are invariably present and the first pair always separate the mental from the chinshields. The first three (22%, 30) or the first four (78% of the time, 30) infralabials contact the first pair of chinshields so that the third and fourth or just the fourth contact the second pair. Four to eight (5 ± 1, 27) gulars and preventrals separate the chinshields from 216–222 (218 ± 3, 10) ventrals and 18–22 (21 ± 1, 10) subcaudals in females and 211–220 (216 ± 3, 12) ventrals and 20–23 (21 ± 1, 12) subcaudals in males. Some entire subcaudals are invariably present on the proximal one-third of the tail and number from 2–8 (4 ± 1, 26).

The rostral, nasals, internasals, and prefrontals have black blotches and edging. A subrectangular black blotch lies in each prefrontal. A well-defined black interorbital band is angled anterolaterally across the eye and onto supralabial 3 and the upper edge of (4) It overlaps about one-half to three-fourths of the supraoculars and frontal. The parietals may be immaculate (e.g., CM 126, 2828) or have black apices (e.g., CM 2841, 2952) in specimens from Santa Cruz. A specimen from Pando (NK 259) closely resembles upper Amazonian specimens of *Micrurus obscurus* in being more melanic overall and in having a single large blotch in the center of each parietal. Each parietal is almost one-half black because of greatly enlarged black apices in UMMZ 60733 from Buena Vista, SC. The mental is mostly to completely black and, frequently, the first one or two infralabials have black edges. The rest of the gular region is nearly to completely immaculate.

There are 6–9 (7 ± 1, 31) triads on the body and usually (93%, 31) two-thirds of a triad on the tail. Two specimens (MCZ 24895, UMMZ 60777, 7%, 31) have a complete triad on the tail. The first triad is two-thirds and the first black ring is a middle ring. "Remnants" of the "missing ring" are seen as a row of prominent black apices in a line just behind the rictus and crossing the first vertebral. In Bolivian specimens, a black gular band is usually absent, however some of the lateral gular scales may have black apices, and a poorly defined gular band 2 scales long at midventer is present in NK 259 and CBF 1011. The first black ring on the neck strongly projects anteriorly for 5–11 (7 ± 1, 23) vertebrals and shortens ventrally to 1–3 ventrals. It is separated from the parietals by 0–3.5 (1.4 ± 0.6, 30) yellow vertebrals. In CBF 1011, the first black ring is particularly long and reaches the parietals. The second ring is only somewhat shorter to almost one-half as long ventrally. Elsewhere on the body and tail, black rings are consistently longest vertebrally and constricted on the flanks. Midventrally, the first and last black rings of some triads project into the center of the first and last yellow ventral. A few (1–7) black rings are incomplete ventrally. In most specimens, the last black ring in front of the cloaca is incomplete or altogether absent.

The red rings bear some diffuse speckling or some faint, black apical tips. In the specimen from Pando, all except the first two rows of dorsals bear black apical tips. However, the amount of black in the red scales of this specimen is only about one-third as much as in the yellow scales. The yellow scales have heavy black apices in all specimens.

*Micrurus obscurus* is often characterized as having yellow rings longer than the black rings. However, the exterior black rings are one-half to one vertebral longer than the yellow rings in seven specimens; both the exterior and middle black rings are longer than the yellow rings in FMNH 35733. At midbody, the red rings are 6–11.5 (8 ± 2, 28), the exterior black rings 3–6 (4 ± 1, 28), the yellow rings 3.5–7.5 (5 ± 1, 28), and the middle black ring 3–5 (4 ± 0.5, 28) vertebrals long. The middle black rings are 35–75% (54 ± 1, 28) as long as the red rings. The exterior black rings are 67–125% (105 ± 21, 28) and the yellow rings are 80–187% (119 ± 24, 28) as long as the middle black ring.

*Distribution and Comparative Material.—Micrurus obscurus* occurs in the upper Amazon basin from Colombia and Southern Venezuela to the vicinity of Santa Cruz de la Sierra (Fig. 9).

**BOLIVIA. BENI. Gral. José Ballivián:** Rurrenabaque (AMNH 22498). **Moxos:** Oromomo (CBF 1011). **Vaca Diez:** Riberalta (NK 512). **PANDO. Nicolás Suárez:** San Carlos (NK 259). **SANTA CRUZ. Andrés Ibáñez:** Santa Cruz de la Sierra (CM 126), Terevinto (NK 483). **Ichilo:** Río Saguayo, Parque Nacional Amboró (NK 158), Río Surutú (UMMZ 63818–63819), "Río Pitasama a 14 km desde el Río Surutú," Parque Nacional Amboró (NK 440), Buena Vista [AMNH 35985, CM 2763, MCZ 24895, FMNH 35729, FMNH 35731, FMNH 35733, UMMZ 60733, UMMZ 60776–60777, UMMZ 60779, UMMZ 60781, UMMZ 63816 (n = 2), UMMZ 63818, UMMZ 67929–67930], Río Surutu, W of Buena Vista (CM 2841), Río Colorado (CM 2952), unknown (CM 2961). **UNKNOWN:** CM 2828, NK 2023–24.

**ECUADOR. MORONA-SANTIAGO:** USNM 232481. **NAPO:** USNM 232482–83. **PASTAZA:** USNM 232491–93, USNM 287947–50. **UNKNOWN:** FML 1693.

**PERU: HUANUCO:** USNM 193724–29.

*Remarks.*—Eastern Bolivia may be the only location where species of the *Micrurus spixii* complex are in sympatry (Fig. 9). If the status of these taxa is to be established, conclusions will necessarily have to be based on the samples from Bolivia.

Three characters have been used to distinguish the subspecies of *Micrurus spixii*: number of body triads and length and position of the black nuchal ring. Among specimens we examined, there is more overlap in the first two of these characters than Schmidt's (1953*b*) and Roze's (1996) keys and accounts would lead one to believe. The nuchal ring extends for eight or more (up to 11) vertebrals in fifty percent of the specimens from the vicinity of the type locality of *M. s. princeps* (Santa Cruz de la Sierra), so that these specimens key out to *M. s. obscurus* in Roze's key. Roze (1996, his couplet 1, p. 215) characterizes the nuchal ring of *obscurus* as extending for 8 or more dorsals and that of *princeps* as extending for seven or fewer. Schmidt (1953*b*) used number of body triads to separate *M. s. obscurus* and *M. s. princeps*. However, as Schmidt's data (top of his page 178) indicate, overlap among these putative subspecies is considerable: 29% of the *M. s. obscurus* he examined had 6–7 body triads, the most common (90% of Schmidt's specimens) condition in *M. s. princeps*. *Micrurus s. martiusi* and *M. s. spixii* have the nuchal ring covering the parietals and are separated by Roze (1996) and Schmidt (1953*b*) on the basis of numbers of body triads. Again these ranges overlap. In Roze's key, *M. s. martiusi* is characterized as having six to eight complete triads on the body, *M. s. spixii* as having four to six complete triads. Interestingly, although Schmidt (1953*b*) and Roze (1996) assigned Bolivian

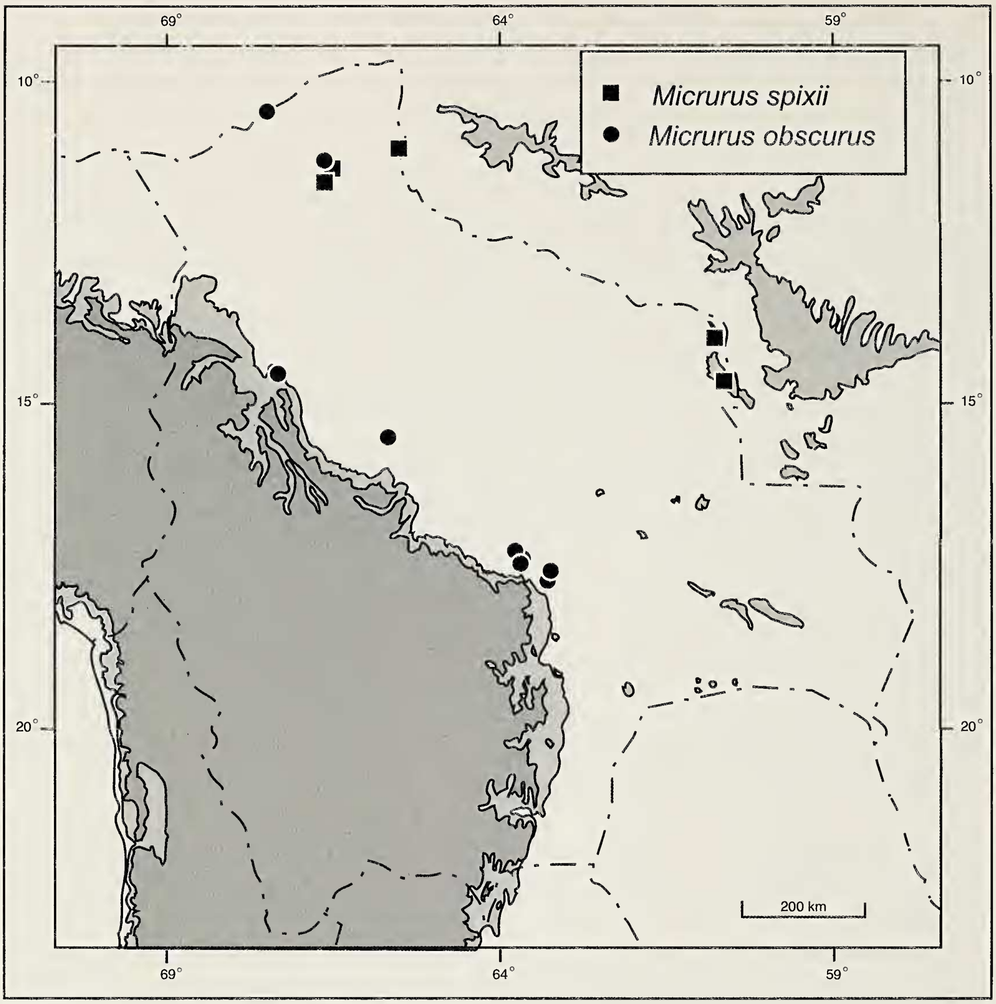

Fig. 9.—Distribution of the *Micrurus spixii* complex in Bolivia.

specimens to *M. s. spixii*, all but one (AMNH 22277) of the specimens we examined had seven or more body triads, thus keying out to *M. s. martiusi*. Roze's (1996) map provides dot localities for four specimens which he suspected were intergrades (two referred to "*M. s. spixii x princeps*" and two referred to "*M. s. obscurus x princeps*"). Unfortunately, he did not cite specific specimens or explain why these specimens were classified as intergrades, and we could not evaluate their status.

In Bolivia, two clearly distinct species have been referred to *Micrurus spixii*. As we argue above, the differences between *M. s. obscurus* and *M. s. princeps* on the one hand and between *M. s. martiusi* and *M. s. spixii* on the other have been overstated or, at least, accorded too much significance. We therefore refer *Elaps princeps* Boulenger to the synonymy of *Micrurus obscurus* (Jan) **new combination** and *Micrurus spixii martiusi* Schmidt to the synonymy of *Micrurus spixii* Wagler. In Bolivia, these two species have been found in sympatry at Riberalta, Beni department (compare NK 512 and UMMZ 63820). Two additional specimens, *M. spixii* from Tumi Chucua, Beni (USNM 280426) and *M. obscurus* from San Carlos, Pando (NK 259) are both from within 100 km of Riberalta. There is no apparent intergradation between these species in Bolivia where their ranges overlap.

The two species are easily separated on the basis of pattern. *Micrurus obscurus* differs from *M. spixii* in having a black interorbital band angled anteriorly where it crosses the eye and overlapping supralabial 3 and part of 4 (Fig. 8; see also Fig. 34 in Schmidt, 1953*b* and species accounts in Roze, 1996). The band is not present in *M. spixii*, and the anterior 1–5 supralabials have black posterior edges. The dorsal head scales in *M. spixii* are black with red or yellow margins and the parietals are nearly completely black. In *M. obscurus*, the snout scales are yellow with black margins and spots. In central Bolivia, the parietals of *M. obscurus* are immaculate or have black apices, whereas large black spots are present in the parietals of specimens from northern Bolivia and elsewhere in upper Amazonian South America. The first black ring on the body of *M. spixii* is an exterior ring and has a nearly vertical anterior margin, whereas the black ring is a middle ring and strongly projects anteriorly in *M. obscurus* [the first triad is occasionally complete in specimens from the Orinoco drainage of Colombia (Campbell and Lamar, 1989; Roze, 1996), however this condition has not been observed in Bolivia]. Finally, the mental and sometimes the flanking first or second infralabials are black and the posterior ventral surface of the head is immaculate in Bolivian *M. obscurus*. In the other subspecies, the pattern on the chin is quite different, with black blotches being most prominent on more posterior infralabials. Some specimens (e.g., AMNH 22277) of *M. spixii* also have a black mental. All but 2 (93%) of our sample of Bolivian *M. obscurus* have two-thirds of a triad on the tail, whereas most (57%) Bolivian *M. spixii* have one to one-and-a-third triad on the tail. Finally, some (1–7) exterior rings are incomplete and others are noticeably very short ventrally in Bolivian *M. obscurus*. Ventrally, the black rings are as long as or longer (e.g., USNM specimens) than they are dorsally and they are always complete on the body in *M. spixii*. As for other species of coralsnakes, rings in *M. spixii* may be incomplete (e.g., USNM 280426) when they traverse the vent.

Intraspecific concordance in several characters and sympatry between *M. spixii* and *M. obscurus* in Beni strongly indicates that these species do not interbreed. Contra Roze (1996), we do not believe that a case for intergradation has been made, and we have not observed any evidence of intergradation between these two well-differentiated and recognizable species.

*Micrurus obscurus* (as *M. spixii princeps*) has long been thought to be the largest coralsnake based upon measurements of CM 126. Griffin (1916) reported 1602 mm for this specimen and Schmidt (1953*b*) reported 1600 mm. These measurements are incorrect by more than 150 mm; this male specimen is 1413 mm (SVL 1345 mm, tail length 68 mm). A specimen of *Micrurus ancoralis* in the BMNH measured 1486 mm and may be the largest coralsnake (Roze, 1996).

### *Micrurus pyrrhocryptus* (Cope)
(Fig. 10)

*Elaps pyrrhocryptus* Cope, 1862:347. HOLOTYPE (sex unknown) from "Vermejo River, Argentine Chaco" (=Río Bermejo, Chaco, Argentina, Scrocchi, 1990) (ANSP 5395). Peracca, 1895:19; Berg, 1898:29.

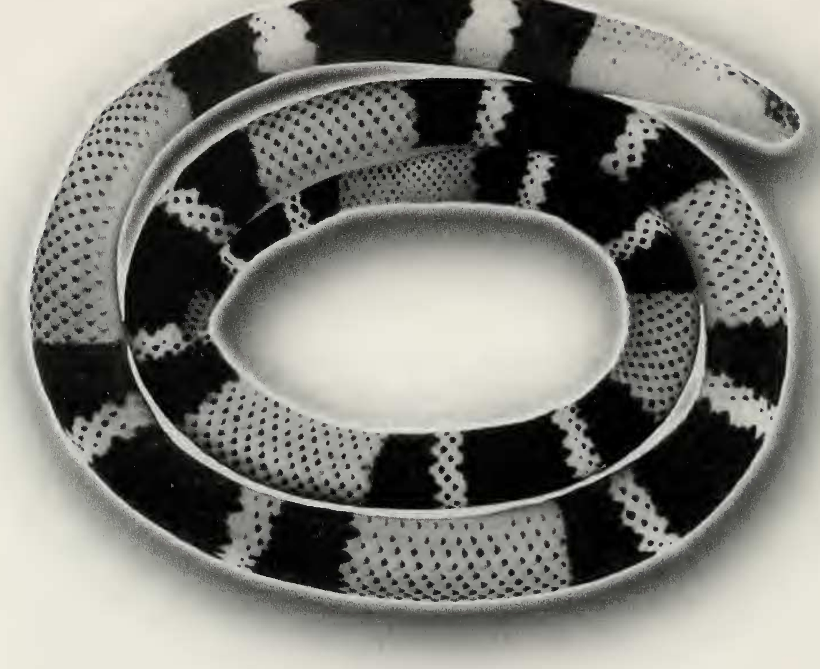

Fig. 10.—*Micrurus pyrrhocryptus* (UTA 51404) from Finca Dos Milanos, Chiquitos, Santa Cruz.

*Elaps marcgravii* (Wied-Neuwied): Boulenger, 1896:428; Peracca, 1897*b*:15.
*Elaps Simonsii* Boulenger, 1902*a*:338. HOLOTYPE female from "Cruz del Eje," Córdoba, Argentina (BMNH 1946.1.21.33).
*Elaps frontalis* (Duméril, Bibron, and Duméril): Lönnberg, 1902:461; Amaral, 1925:19; Bucher, 1980: 158.
*Micrurus pyrrhocryptus* (Cope): Schmidt, 1936:199; Hoge and Lancini, 1960:12; Scrocchi, 1990:359; Cruz et al., 1992:104; Yanosky et al., 1993:163; Lavilla et al, 1995:126; Gonzales, 1998:49; Leynaud and Bucher, 1999:37; David and Ineich, 1999:152; Jorge da Silva and Sites, 1999:172.
*Micrurus lemniscatus frontalis* (Duméril, Bibron, and Duméril): Amaral 1944:92 (in part); Abalos and Nader, 1962:83; Abalos et al., 1964:267; Abalos and Mischis, 1975:74.
*Micrurus frontalis pyrrhocryptus* (Cope): Shreve, 1953:5; Barrio and Miranda, 1967:872; Roze, 1967: 26; Roze, 1970:209; Hoge and Romano, 1973:125; Laurent and Teran, 1981:13; Roze, 1983:326; Golay, 1985:34; Campbell and Lamar, 1989:116; Golay et al., 1993:168.
*Micrurus tricolor* Hoge, 1956:67. HOLOTYPE male from "Garandazal" (=Carandazal according to Jorge da Silva and Sites, 1999), Mato Grosso do Sul (IB 16290). Strussman and Sazima, 1993: 163; Jorge da Silva and Sites, 1999:176. [**revised synonymy,** see remarks]
*Micrurus lemniscatus* (Linnaeus): Abalos, 1961:70.
*Micrurus fontalis* (Duméril, Bibron, and Duméril): Fugler, 1986:57; Fugler and Cabot, 1995:60.
*Micrurus frontalis tricolor* (Hoge): Campbell and Lamar, 1989:116; Golay, 1993:168.
*Micrurus pyrrhocryptus pyrrhocryptus* (Cope): Roze, 1994:179; Roze, 1996:212.
*Micrurus pyrrhocryptus tricolor* (Hoge): Roze, 1994:179, 1996:212.

*Diagnosis*.—(1) Dorsal pattern of white, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) first triad complete; (7) 5–12 red vertebrals separating first triad from parietals; (8) all dorsal head scales including parietals black, edged in white; (9) red rings with heavier black apices than white rings; (10) white rings longest dorsally, constricted or broken ventrally by black rings; (11) chin red with no to moderate black mottling and edging of scales; mental mostly or entirely red; (12) 6–14 triads on body, 1–1.67 on tail.

*Description.*—(Based on 9 females, 11 males, and 5 juveniles). *Micrurus pyrrhocryptus* is a large species; specimens in our sample were 264–1209 mm long (Jorge da Silva and Sites, 1999, report a maximum size of 1241 mm), the largest specimen being a male. The tails of females are 6.2–7.4% (6.7 ± 0.4, 8) as long as their snout-vent lengths, and the tails of males are 5.9–8.1% (7.2 ± 0.9, 10) as long as their snout-vent lengths. The head accounts for 1.5–2.4% (2.2 ± 0.3, 22) of snout-vent length.

In our sample, all specimens had 2/2 postoculars and 1+1/1+1 temporals. One specimen had eight infralabials on one side only, whereas all others had 7/7 infralabials and supralabials. The prefrontals contact the supralabials in a single specimen (NK 882). Eye-nostril distance accounts for 18–37% (23 ± 5, 15) of head length, and eye diameter accounts for 12–27% (16 ± 5, 14) of head length. In this species, the supraocular is usually narrower than the frontal. However, the supraocular was 0.1 mm wider in one specimen (NK 2031). Variation in relative widths of these scales is considerable: the supraocular is 70–103% (84 ± 8, 16) as wide as the frontal.

In three of our specimens (12%, 25), only the first three infralabials contact the first pair of chinshields on both sides; more often, the first four contact the first pair and only the fourth contacts the second pair. Four to six (5 ± 1, 25) gulars and preventrals separate the second pair of chinshields from the ventrals. Females have 221–240 (229 ± 5, 9) ventrals and 20–26 (24 ± 2, 8) subcaudals, whereas males have 220–246 (234 ± 8, 12) ventrals and 24–31 (28 ± 2, 12) subcaudals. In three specimens (12%, 25) one to as many as nine subcaudals were entire.

The dorsal head and snout scales (internasals, prefrontals, frontal, parietals, oculars, nasals, rostral) are black with white bordering. Usually, the centers of these scales are immaculate, although white blotches may be present on some scales (e.g., AMNH 141357, white blotch on one prefrontal). The first three or four supralabials are mostly black with white margins. The temporals and last three supralabials range from being immaculate red (e.g., AMNH 141357) to having large black blotches (e.g., MCZ 20622). The infralabials, chinshields, and gulars are red and may be nearly immaculate (UTA 51404) or have diffuse to moderate (MCZ 20622) amounts of black blotching and edging of scales. The mental may also have some black pigment, but it is mostly red.

The black rings are longest ventrally where they project into the white rings, usually constricting them to one or two ventrals. Except rarely (e.g., CM 2761; AMNH 141357), the white rings are complete; the black rings are always complete. Bolivian specimens have about the same number of body triads as conspecifics in Argentina and Paraguay (Jorge da Silva and Sites, 1999), however the distance to the first triad appears to be greater (Jorge da Silva and Sites, 1999, do not give a mean value for this meristic but provide a range of 5–7 vertebrals from the parietals to the first black ring). Two specimens (CBF 1203 with 12 and USNM 1186 with 14 body triads) had more than 11 body triads. In Bolivia, this species has 6–14 (8 ± 2, 25) triads on the body and 1–1.67 (usually 1.33, 25) triads on the tail. The first triad is separated from the parietals by 5–11.5 (8.5 ± 2.5, 25) vertebrals.

The statement that "the middle black ring is at least twice (10–14 dorsal scales) the length of the external one (5–7 dorsal scales)" (Jorge da Silva and Sites, 1999, p. 174) does not apply to this species in Bolivia where relative lengths of the rings are highly variable. In one specimen (USNM 1186), the middle black rings (3 vertebrals long in the middle triad) were about the same size to slightly shorter than the external black rings (3.5 vertebrals long in the middle triad). The external rings were 2.5–5.5 dorsals long and 32–117% (62 ± 21, 24) as long as the middle ring, which ranges from 3–11 vertebrals. Moreover, the red rings are never "almost the same length as the entire triads" (contra Jorge da Silva and Sites, 1999, p. 174). In three specimens (e.g., NK 524), the middle black rings and the red rings are about the same length. In the entire sample, red rings are 7.5–15.5 dorsals long, and the middle black rings are 22–107% (65 ± 21, 24) as long as the red rings. The white rings are 1–3.5 vertebrals long and 36–105% (60 ± 21, 24) as long as the external black rings.

*Distribution*.—Jorge da Silva and Sites (1999) discuss this species' distribution outside of Bolivia. Within Bolivia, *Micrurus pyrrhocryptus* is restricted to the Gran Chaco, the band of high forest of the Tierras Bajas region, Chiquitanía, and the vicinity of Santa Cruz de la Sierra and Buena Vista (Fig. 11). In addition to our localities, Lönnberg (1902) examined specimens from "Tatarenda, Caiza, Bolivian Chaco" and Roze (1983) reported that the species occurs in lowlands near the type locality of *M. diana*.

**BOLIVIA. CHUQUISACA. Luis Calvo:** Pozo Camatindi (CBF 1203). **SANTA CRUZ. Andrés Ibáñez:** Santa Cruz de la Sierra (NK 511, 728, 882, 961, 1447). **Chiquitos:** NK 2035, UTA 51404 (Finca Dos Milanos). **Cordillera:** Aguaraigua (NK 1446), Camiri (USNM 118640), Izozog (NK 2025–26, NK 2031–32), 1 km N Gutiérrez (NK 543 (1 Km N of Gutiérrez). **Ichilo:** Buena Vista (CM 2760, 2761, FMNH 16788, MCZ 20622). **Ñuflo de Chávez:** Estancia San Miguelito (NK 1308). **Sara:** unknown (CM 2762). **Warnes:** Azusaquí (NK 125). **Unknown:** UMMZ 69553. **UNKNOWN:** NK 524, 654.

*Remarks*.—Although long considered to have its affinities with snakes of the *Micrurus frontalis* complex, the status of Hoge's (1957) *Micrurus tricolor* has been the subject of debate. It has been considered a separate species (Strussman and Sazima, 1993; Jorge da Silva and Sites, 1999), a synonym of *M. pyrrhocryptus* (Hoge and Lancini, 1960; Scrocchi, 1990), or a subspecies of either *M. frontalis* (Roze, 1983; Golay, 1985; Campbell and Lamar, 1989) or *M. pyrrhocryptus* (Roze, 1994; 1996).

Jorge da Silva and Sites (1999) provide a thoughtful review of the *Micrurus frontalis* complex. Refreshingly, their analysis is based on carefully defined methodological procedures and clear statements as to their concept of species. The number of specimens examined by the authors and their lab assistants is impressive. Most of the specimens examined in their study (many in Brazilian museums) were not included in this study; however we did examine the same specimens in the Museo "Noel Kempff Mercado," the Fundación Miguel Lillo, and several museums in the United States.

In most instances, we agree with the findings of Jorge da Silva and Sites (1999); however, they are incorrect regarding the distinctiveness of *Micrurus tricolor*. Jorge da Silva and Sites (1999) took issue with the opinions of some revisors, stating, "the biggest problem in accepting Scrocchi's (1990) and Roze's (1994, 1996) taxonomic arrangement is that *M. tricolor* is not an isolated population in Mato Grosso do Sul, but it extends into Bolivia where it is sympatric with *M. pyrrhocryptus* and possibly *M. diana*." This statement is based on a single Bo-

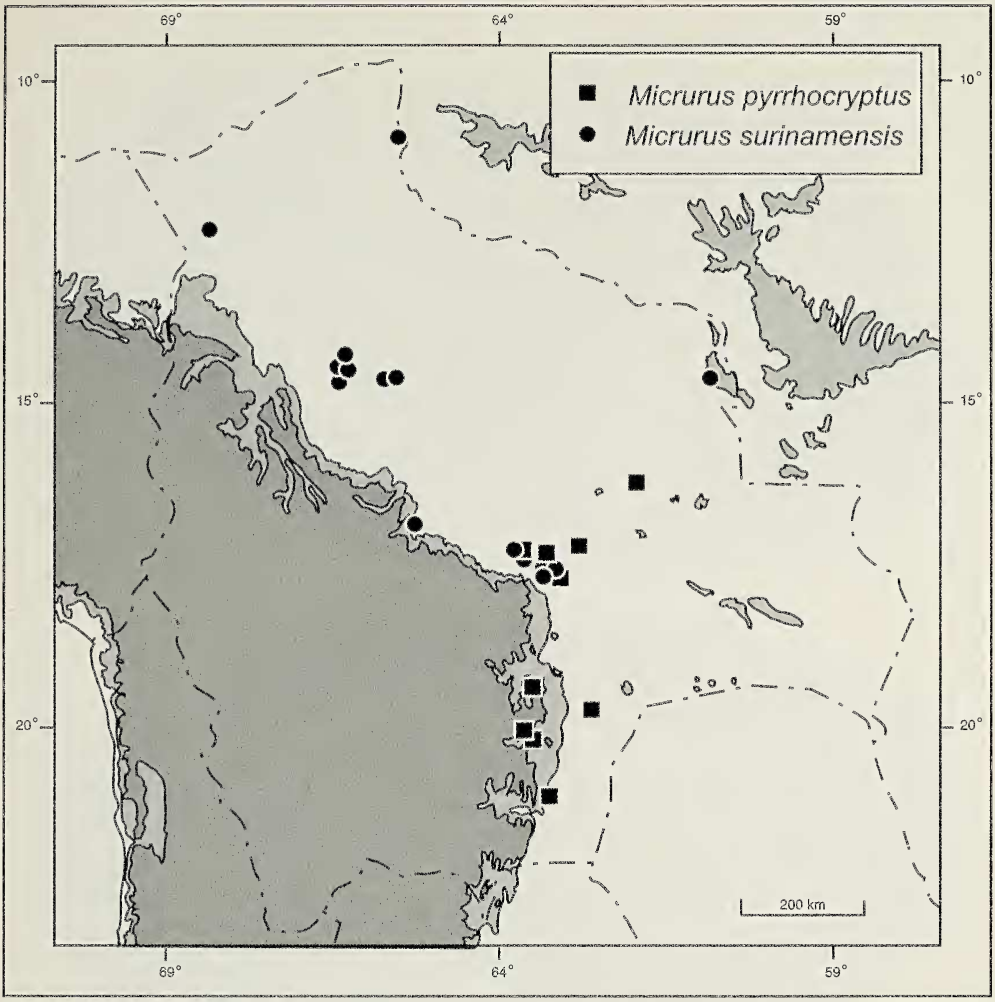

Fig. 11.—Distribution of *Micrurus pyrrhocryptus* and *M. surinamensis* in Bolivia.

livian specimen that these authors referred to *M. tricolor*: NK 543 (Fig. 12) from 1 km N. of Gutiérez, Santa Cruz, Bolivia.

This specimen (NK 543) does not have diagnositic features of *Micrurus tricolor* (characters from Jorge da Silva and Sites, 1999, of *M. tricolor* in parentheses) that might be used to distinguish this species from *M. pyrrhocryptus*. All of the black snout scales have prominent white margins ("black snout covering all scales with very little white bordering, which when present is mostly restricted to the supralabials" and "frontal, supraoculars, and parietals are completely black"). Nearly all white scales in the triads have black tips (white scales in triads "immaculate"). In NK 543, the first triad is separated from the parietals by 8 dorsals, and this value is one scale higher than the narrow range of 5–7 dorsals Jorge da Silva and Sites (1999) report for *M. pyrrhocryptus*. However, variation in this character is much greater than the data of Jorge da Silva and Sites (1999) indicate.

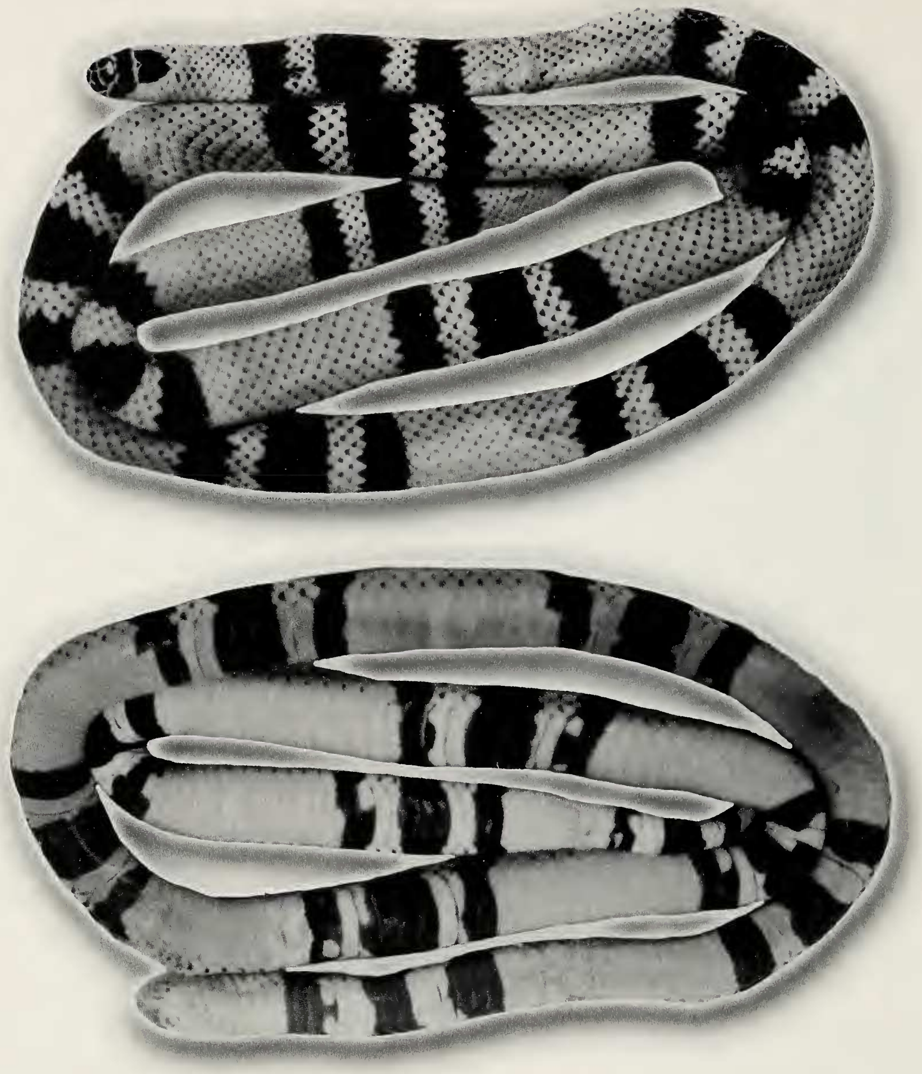

Fig. 12.—Specimen of *Micrurus pyrrhocryptus* (NK 543 M) misidentified as *M. tricolor* by Jorge da Silva and Sites (1999).

Among our sample, the parietals are separated from the first triad by 4–16 dorsals (8 or more dorsals in 59% of the specimens).

If sympatry of the two species is the real "problem" with synonymization, we wonder why no Bolivian *Micrurus pyrrhocryptus* were examined by Jorge da Silva and Sites (1999, see their appendix) when the same authors visited museums (e.g., Museo Noel Kempff) or at least borrowed specimens from museums (MCZ, FML) containing specimens of Bolivian *M. pyrrhocryptus*.

We have established that these two taxa are not sympatric and that *Micrurus tricolor* is not known from Bolivia. The remaining question is whether characteristics of the isolated Mato Grosso population are distinctive enough to warrent its recognition as a full species. Our concept of species is equivalent to that voiced by Jorge da Silva and Sites (1999; see also Frost and Hillis, 1990), and we have few complaints about their use of concordance (Avise and Ball, 1990) as a criterion for recognizing species. From Jorge da Silva and Sites' monograph, readers will conclude that *M. tricolor* could be recognized as distinct from *M. pyrrhocryptus* due to concordance of two characters: black snout scales with very little white bordering (vs. prominent white bordering in *pyrrhocryptus*) and white rings "immaculate" (vs. white rings "always black tipped"). Characterizations of the amount of black pigmentation in the rings are somewhat exaggerated. Frequently in *M. pyrrhocryptus* (e.g. NK 2031–32; UTA 51404), the first white ring is nearly immaculate, the second ring has a few short black apices, and more posterior white rings have increasing amounts of black. Only on the posterior one-third of the body and on the tail does every white scale possess a black apex (see also, Fig. 27b and c of Sites and Jorge da Silva, 1999). Similarly, some white scales have black apices increasingly on the posterior portion of the body of *M. tricolor*. Scales with black apices are clearly visible in all but the first two triads of the holotype (figure 1 on p. 71 of Hoge, 1957, and figure 31 of Jorge da Silva and Sites, 1999). The amount of black apices present in white rings is notoriously variable within many species of coralsnakes: *M. frontalis* (Jorge da Silva and Sites, 1999), *M. lemniscatus* and *M. serranus* (this study), to name a few. Extent of white bordering of dorsal head scales is quite variable in several species of the *M. frontalis* complex. Regional variation in these traits should be expected.

Jorge da Silva and Sites (1999) use multivariate analyses to support their taxonomic conclusions, and the results of these analyses are illustrated in their figure 2. In this figure, the error bars for females of *Micrurus pyrrhocryptus* and *M. tricolor* overlap substantially along both canonical variables. Males are partially separated along canonical variable 1 only. Inspection of the eigenvalues in table 3 of Jorge da Silva and Site's study shows that this variable is most influenced by middle black ring length and total number of triads. Jorge da Silva and Sites report that these same two variables were negatively correlated in a univariate analysis, and this fact explains the opposite signs of the corresponding eigenvalues. Essentially, the two variables seem to be a redundant expression of the same phenotypic trait: increase in number of triads requires that the middle black rings be shorter. The multivariate techniques do not uncover differences in these putative species. Above, we call attention to overlap in the error bars of females. We also point out that number of triads (and, therefore, length of the middle black ring) is much more variable in *M. pyrrhocryptus* than Jorge da Silva and Sites' data indicate, so that the apparent separation of males for canonical variable 1 would likely break down with the inclusion of more data.

Between *Micrurus pyrrhocryptus* and *M. tricolor*, only minor differences in coloration remain as potentially diagnostic characters: the amount of white bordering of the head scales and the amount of black pigment in the rings differ in degree only. Contrary to the claims of Jorge da Silva and Sites (1999), these taxa do not occur in sympatry, and we see no compelling evidence for recognition of them as distinct species. We follow Roze (1983, 1994, 1996), Golay (1985), and Campbell and Lamar (1989) in recognizing the Mato Grosso population as a subspecies: *Micrurus pyrrhocryptus tricolor* (Hoge).

As pointed out in the description, several meristics of the Bolivian specimens are at odds with Jorge da Silva and Sites' (1999) characterization of *Micrurus pyrrhocryptus*. The most atypical specimen in our sample (USNM 118640) was collected by Raymond M. Gilmore from "Camiri, 5 km S of Chorati, 800 m" (=Choreti) in the Gran Chaco of southern Santa Cruz. This specimen is unusual in having 14 body triads and the external black rings being the same size or slightly longer than the middle black ring.

We assign the specimen to *Micrurus pyrrhocryptus*, because its dorsal head and snout scales are black edged in white, seven vertebrals separate the first triad from the parietals, and the red and white rings have prominent black apices. In their diagnosis, Jorge da Silva and Sites (1999) state that *M. pyrrhocryptus* has 6–11 body triads, however in their remarks they say "the sample of *M. pyrrhocryptus* included in this study shows only three specimens with 12, 13, and 14 body triads respectively, and the majority of specimens have between 6 and 11 triads." Therefore, the diagnosis is misleading and should have included the known range of body triads with a qualifying statement that the species usually has 6–11 triads. We doubt that the USNM specimen is either *M. frontalis* or *M. baliocoryphus*, because the known distributions of both species are very distant from Camiri. These species reportedly differ from *M. pyrrhocryptus* in having white chins, however the USNM specimen is in poor condition, and we cannot determine the original color of its chin. Jorge da Silva and Sites (1999) fail to provide information on two potentially diagnostic features of *M. baliocoryphus*: number of vertebrals to the first triad and presence or absence of black pigment in the white rings. They state that in *M. baliocoryphus* the middle black ring is "at least twice as long" as the external black rings, however this statement is almost certainly an exaggeration as seems to be the case for a similar claim regarding *M. pyrrhocryptus*. The statement is not consistent with specimens Jorge da Silva and Sites examined. In FML 1986 (formerly CHINM 2870. The Colección Herpetologica del Instituto Nacional de Microbiología Carlos G. Malbrán gave this specimen to the Fundación Miguel Lillo, and the two tag numbers do not apply to separate individuals as Jorge da Silva and Sites thought, p. 164), the middle black ring is only slightly longer (2.5 vertebrals) than the external rings (2 vertebrals). Regarding this specimen, Jorge da Silva and Sites (1999, p. 164) write "The specimens (CHINM 2870 M and CHINM 2871 M) mentioned by Scrocchi (1990) as intermediary forms are in fact *M. baliocoryphus*, and this has been corroborated by an additional specimen (FML 1986 M)." Like *M. altirostris*, the external and middle black rings are about the same size, and, on the basis of this character, Scrocchi's (1990) opinion is understandable. In the FML specimen, the white rings of the first two triads are nearly immaculate, but in the remaining triads about one-half to two-thirds of the white scales have prominent black apices (i.e., some white rings are as heavily pigmented as the red rings). Except for relative widths of the rings, the specimen has the characteristics of *M. baliocoryphus*: 3.5 vertebrals separate the parietals from the first triad (vs. 1–2 in *M. altirostris*), the chin has only moderate amounts of black pigment (heavy in *M. altirostris*), and there are 11 (vs. 13–18 in *M. altirostris*) body triads.

## *Micrurus serranus*, **new species**

(Fig. 6 A, 6C, 13)

*Micrurus frontifasciatus* (Werner): Campbell and Lamar, 1989: 116 (in part), figure 55; Fugler and Cabot, 1995: 60; Roze, 1996: 175 (in part), color plate 28. **[new synonymy]**

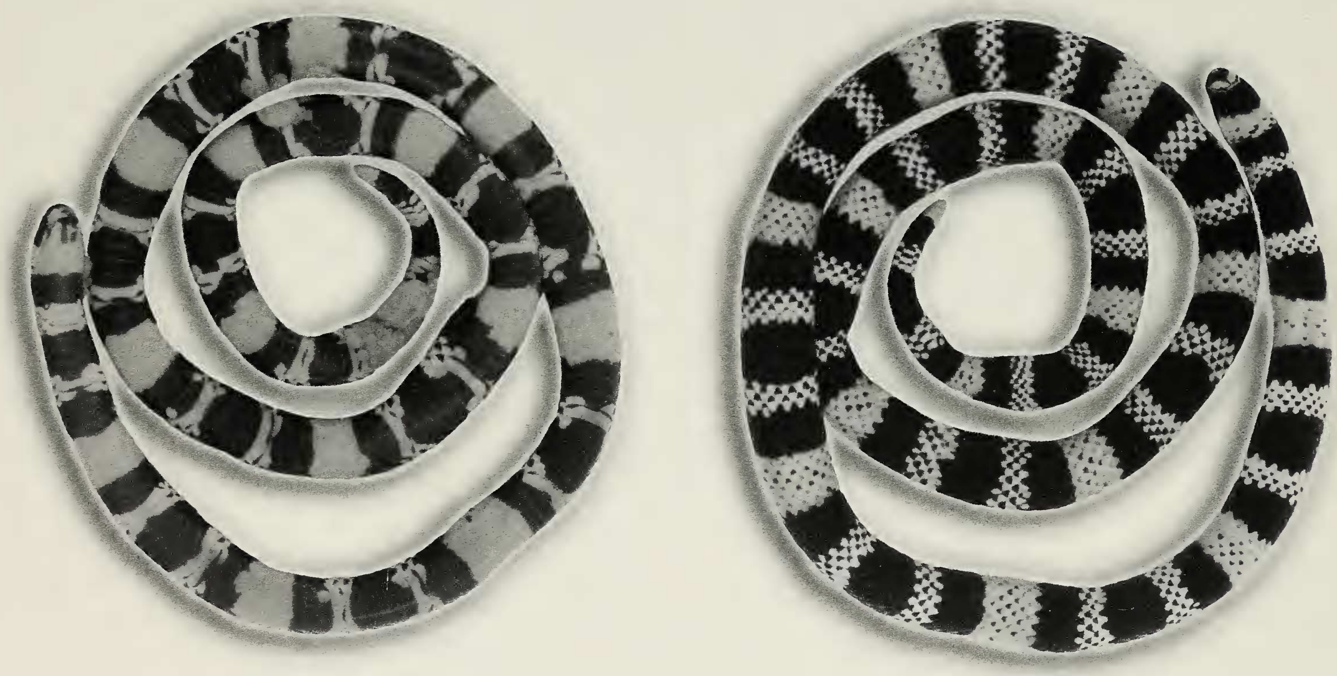

Fig. 13.—*Micrurus serranus* new species (Holotype, UTA 34561 M) from 3 km N of Samaipata, Florida, Santa Cruz.

*Holotype.*—A male specimen, UTA 34561 (collector's tag M. B. Harvey 1960) found by Michael B. Harvey, 3 km N of Samaipata on the road to Mairana, Florida Province, Santa Cruz, Bolivia, 14 Feb. 1992.

*Paratypes (39).*—Museum numbers are followed by the specimen's sex, its collector, date collected, and locality. The canton within Florida province follows the specific locality when that locality could not be located in the *Atlas Estadístico de Municipios* (Fig. 5). **BOLIVIA. SANTA CRUZ. Caballero:** NK 1565 (M, A. Medellín, 4 Feb. 1998, San Juan del Potrero), NK 2020 (F, S. Medellín, 26 Nov. 1999, San Juan del Potrero). **Florida:** UTA 34562 (F, M. Harvey, 13 Feb. 1992, Yungas near Mairana, 18.09°, 63.91°W) NK 636 (F, W. Romero, 24 Oct. 94, Pampa Grande), 981 (F, S. Zambrana, 5 Dec. 1996, Algodonal), 1317 (F, N. Ferrufino, 22 Mar. 1997, Mairana), 1442 (F, G. Cardoso, 27 Aug. 1997, Agua Clara, Mataral), 1472 (F, M. Mendoza, 8 Nov. 1997, Algodonal), 1508 (M, I. Diaz, 22 Oct. 1997, Mataral), 1510 (M, M. Cuéllar, 13 Mar. 1998, Mairana), 1517 (M, D. Guzmán, 18 Jan. 1998, Zanjón, Mataral), 1551 (F, A. Langer, 26 Dec. 1997, Mairana), 1552 (M, Z. Rodriguez, 28 Feb. 1998, Becerros), 1555 (M, F. Morón, 6 Dec. 1997, "Villa Merced" = Villa Mercedes, Mataral), 1556 (M, F. Langer, 6 Dec. 1997, Pampa Grande), 1557 (M, A. Rodriguez, 25 Dec. 1997, Becerro), 1558 (F, T. Sejas, 13 Feb. 1998, Zanjón, Mataral), 1561 (F, A. Gutiérrez, 22 Nov. 1997, Pampa Grande), 1564 (M, J. Chilo, 23 Dec. 1997, Palmasola), 1581 (M, I. Zambrana, 29 Nov. 1997, Algodonal), 1584 (F, T. Sejas, 8 Nov. 1997, Zanjón, Mataral), 1587 (F, M. Olmos, 31 Oct. 1997, "Villa Merced" = Villa Mercedes, Mataral), 1589 (F, A. Alaudio, 28 Mar. 1998, Algodonal), 1605 (M, S. Rojas, 6 Jan. 1998, El Millo), 1617 (M, O. Calla, 12 Mar. 1994, Pampa Grande), 1706 (F, A. Langer, 9 Mar. 1997 "entre Mairana y Samaipata"), 1721 (M, A. Ayala, 7 May 1998, Mataral), 1723 (M, N. Terrazas, 8 Apr. 1998, "Villa Merced" = Villa Mercedes, Mataral), 1746 (F, I. Zambrana, 5 Apr. 1998, Algodonal), 1752 (M, W. Peña, 11 May 1998, Zanjón, Mataral), 1865 (M, F. Sejas, 10 Jan. 1999, Palmasola), 1866 (M, F. Olmos, 23 Mar. 1998, Pampa Grande), 1867 (M, Z. Rodriguez, 20 Jan. 1999, Becerro), 1868 (M, M. Rojas, 17 Feb. 1998, Pampa Grande), 1869 (M, D. Ayala, 5 Jun. 1999, Santa Rosa de Lima, Palos Blancos), 1944 (F, G. Lazarte, 28 Oct. 1999, Algodonal), 1945 (F, V. Arroyo, 5 Oct. 1999, Pampa Grande), 2009 (F, A. Rojas, 3 Mar. 1998, El Millo, Pampa Grande), 2030 (F, A. Langer, 29 Nov. 1997, Pampa Grande).

*Referred Specimens (67).*—CBF 1743, NK 447, NK 481, NK 494, NK 590, NK 678, NK 694, NK 754, NK 855, NK 868, NK 883, NK 897–98, NK 916, NK 945, NK 982, NK 989, NK 1065, NK 1249–50, NK 1260–61, NK 1318–1323, NK 1424, NK 1441, NK 1471, NK 1502–03, NK 1545–47, NK 1550, NK 1553–54, NK 1559–60, NK 1563, NK 1568, NK 1580, NK 1583, NK 1590, NK 1603, NK 1613, NK 1639–40, NK 1643, NK 1722, NK 1724, NK 1753, NK 1779, NK 1852–53, NK 1893, NK 1949, NK 1963, NK 1979, NK 1988, NK 2000, NK 2007–08, NK 2013, NK 2016.

*Diagnosis.*—*Micrurus serranus* is a small (maximum size to 822 mm total length) coralsnake with the following characteristics: (1) Dorsal pattern of white, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually (95%) separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually (90%) divided; (6) first triad complete; (7) 1–6 red vertebrals separating first triad from parietals; (8) dorsal surface of head black with white (pale yellow in life) band crossing snout; margins of scales within white ring edged in black; parietals partly red; (9) extent of black pigment in red and white rings variable, but white rings with more black pigment than red rings; (10) white rings longest dorsally, constricted or broken ventrally by black rings; (11) parietals red with black pigment concentrated anteriorly; (12) 10–14 triads on the body, 0.67–1.67 on the tail; (13) black rings almost always longer than white rings; (14) black pigment present on mental, anterior infralabials, and chinshields; white or pale yellow pigment may also be present in the same region.

*Comparisons.*—In that all three species have white bands across their snouts, the new species may be confused with *Micrurus lemniscatus* and *M. filiformis* (characteristics in parentheses). Unlike these Amazonian species, the white rings of *M. serranus* are longest dorsally and invaded or interrupted by the black rings midventrally (white rings longest ventrally, not invaded by black rings). Also, scales in the white band across the snout are edged in black (white band across snout immaculate). In addition, the snout of *M. serranus* is noticeably more acuminate than the rounded snouts of *M. filiformis* and *M. lemniscatus* (Fig. 6).

Four species in the *Micrurus frontalis* complex have black and white snouts and, though rarely the case, occasional specimens in the *M. frontalis* complex may appear to have a white band across the snout. Unlike the new species, the parietals are black in *M. baliocoryphus, M. diana, M. frontalis*, and *M. pyrrhocryptus. Micrurus serranus* usually does not show a tendency toward melanism and has fewer triads (10–14 vs. 13–18) than the distantly allopatric species *M. altirostris*. Black pigment is concentrated anteriorly on the parietals of the new species, whereas it is concentrated posteriorly on the parietals of *M. altirostris*. Although *M. brasiliensis* has black pigment concentrated anteriorly in its parietals and has about the same number of triads as the new species, the white rings of *M. brasiliensis* are as long or longer than the black rings and scales within the white rings are edged weakly in black. In the new species, dorsals in the white rings bear heavy black margins and the white rings are usually shorter than the black rings.

Other cis-Andean triadal coralsnakes are either distantly allopatric or morphologically distinct from *Micrurus serranus* (characters in parentheses). *Micrurus decoratus* from the Atlantic coast of Brazil usually has a higher number of body triads (12–19 vs. 10–14) and reduced black pigmentation in the yellow rings (white to pale-yellow rings with heavy black edging of dorsals). *Micrurus hemprichii* has an entire anal plate (divided), black dorsal head scales including the parietals (white band across snout and red and black parietals), and few body triads consisting of long black rings separated by short orange rings (5–10 vs. 10–14 triads with black rings usually slightly longer than white or pale yellow rings). *Micrurus ibiboboca* usually has fewer body triads (7–10 vs. 10–14), and the ventral surface of its head is red except for occasional specimens with black pigment restricted to the mental (chin always with some black pigment on the mental, anterior infralabials, and chinshields). In *M. isozonus*, the snout is black and usually lacks a white band (white band always present), the parietals are red-orange with black apices (red and black with black pigment concentrated anteriorly), the ventral surface of the head is mostly red and white with very reduced black pigment (heavy black pigment), and the triads are separated by red-orange rings (red) and the light colored rings of the triads are yellow (white to pale yellow). *Micrurus obscurus* and *M. spixii* both have fewer body triads (4–10 vs. 10–14) and the first triad is incomplete. *Micrurus surinamensis* has a red head with black-edged scales (black cap with white ring), and fewer body triads (5–8.67 vs. 10–14). In *M. surinamensis*, only one supralabial (two) enters the orbit.

*Description of Holotype.*—The holotype appears to be an adult based on its size relative to other specimens in the type series and because its hemipenes are well developed. The head is round in lateral profile and subacuminate in dorsal aspect. Its length accounts for 2.3% of snout-vent length. The eye is relatively small; its diameter is 13% of head length and its distance to the nostril is 24% of head length. The rostral is about as wide as the mental and 71% as high as wide. It is followed by pentagonal internasals and prefrontals. The internasals contact the postnasal and are 78% as long as wide. The prefrontals are only slightly wider than long and are separated from the supralabials by broad contact between the postnasal and the single, high preocular. The prenasal is twice as large as the postnasal. The frontal is pentagonal and one-half again as long as wide. It is flanked by subrectangular supraoculars, each 1.6 times as long as wide. The parietals are 64% as wide as long and broadly contact the uppermost and largest of two postoculars. They are separated from the supralabials by 1+1 temporals. A single large vertebral fills the space between the parietal tips. The specimen has 7/7 supralabials; supralabial three barely contacts the postnasal, three and four enter the orbit, and six is separated from the the lower postocular by broad contact between the postocular and supralabial five.

The mental is 73% as long as wide and separated from the first pair of chinshields by broad contact between the first pair of infralabials. A weak mental groove, three times as long as the mental, separates the chinshields. The first pair of chinshields is rectangular and relatively short, being 71% as wide as long; the second pair has rounded posterior margins and is 53% as wide as long. There are 7/7 infralabials, the first four contacting the first pair of chinshields and the fourth contacting the second pair. Two gulars and two preventrals separate the chinshields from 218 ventrals and 23 subcaudals. Subcaudals 2–3 and 8 are entire; the anal scale and remaining subcaudals are divided.

In preservative (70% ethanol after buffered 10% formalin), the dorsal pattern consists of white (pale yellow, in life), red, and black rings. The rostral, prenasal, and supralabial 1 are entirely black. A white blotch is present at the anterior juncture of the internasals, and the remainder of these scales is also uniformly black. The first white band on the head is angled antero-ventrally and overlaps the prefrontals, the anterior edge of the frontal, the anterior edge of the supraoculars, the postnasals, and the anterior halves of the preoculars. On one side, the white pigment extends onto the dorsal edge of supralabial two and anterior corner of supralabial 3, whereas on the other side supralabials 1–5 are entirely black. Scales within the white prefrontal band have prominent black edges. A black band follows the white prefrontal band to cross the eye and overlap most of the frontal, the anterior halves of the parietals, most of the supraoculars, one-half of each preocular, the postoculars, the anterior halves of the first temporals, and supralabials 3–5. This band does not extend onto the lower jaw. The remainder of the dorsal surface of the head (i.e., the posterior halves of the parietals, the posterior halves of the first temporals, the second temporals, and supralabials 6–7) is red. Except for the sixth supralabials, the dorsal head scales in the red band have black apices.

Ventrally, the mental and most of the first infralabials and first chinshields are black. A small black blotch is present on each of the second infralabials near the mental groove. Nonmelanic portions of infralabials 1–2 and the first pair of chinshields are white. The remaining scales on the ventral surface of the head are immaculate red.

The first triad is complete and is separated from the parietals by a single red vertebral. Rings in the first triad are symmetrical in size: the exterior rings are three vertebrals long, the white rings two vertebrals long, and the middle black ring five vertebrals long. Ventrally, the first black ring overlaps most of the first preventral and all of the first and second ventrals. There are fourteen triads on the body and one complete triad on the tail. A red ring overlaps the anal plate, and the tip of the tail is also red. Throughout the body and tail, the anterior edge of each black ring is straight, i.e., posterior portions of some white or red scales are overlapped by black rings. However, the posterior edge of black rings appears jagged; black scales are entirely black, and the jagged appearance is due to the staggered arrangement of dorsals. In the white rings most scales bear heavy black apices and edging, whereas only a few scales in each of the red rings bear much weaker black apices and these scales tend to be concentrated vertebrally and in the middle of the red rings. Ventrally, red rings are immaculate. Ventrals and paraventrals of the white rings have black edges. In most triads, a single round white spot is positioned laterally in the last ventral of exterior black rings. The black rings invade the white rings and completely interrupt them in the fifth and sixth triad.

In the middle triad, the red ring is 2.5, the exterior black rings two, the white rings two, and the middle black ring three vertebrals long. The caudal triad is relatively longer than those on the body due to an increased length of the middle ring: whereas, the white and exterior black rings are both three vertebrals long, the middle ring is six vertebrals long.

Measurements (in mm) of holotype: snout-vent length 480, tail length 34, head length 10.90, eye-nostril distance 2.58, eye diameter 1.42, length of red ring in middle triad 5.78, length of exterior black ring in middle triad 5.72, length of white ring in middle triad 4.05, length of middle black ring in middle triad 7.77, rostral width 2.8, rostral height 2.0, internasal width 1.89, internasal height 1.47, prefrontal width 2.24, prefrontal height 2.18, frontal width 2.42, frontal length 3.69, supraocular width 1.9, supraocular length 3.1, preocular height 3.12, preocular length 4.84, mental width 2.19, mental length 1.54, first chinshield width 1.5, first chinshield length 2.12, second chinshield length 2.84, length of mental groove 4.66.

*Variation.*—Except where noted, this section is based on the type series and does not include data from referred material. *Micrurus serranus* usually possesses the cephalic squamation pattern typical of most congeners. Among the type series, 1+1 temporals were usually (94%, 40) present, although three specimens had 1+2 temporals on one side only, and one specimen had 2+2 temporals on one side. One preocular and two postoculars were almost invariably present (NK 1558 had one postocular on one side only), and the supralabials and prefrontal were always separated by contact between the preocular and postnasal. Supralabials and infralabials numbered seven, except in NK 1867 which had six supralabials on one side. Supralabials three and four invariably enter the orbit. In two specimens, the mental contacts the anterior pair of chinshields, but these scales are otherwise separated by medial contact between the first pair of infralabials. Five percent of the time, only the first three infralabials contact the first chinshield; usually, infralabials 1–4 contact the first and infralabial 4 contacts the last chinshield. Four paratypes (10%, 40) had entire anal plates.

Sexual dimorphism could not be demonstrated statistically for relative body and tail lengths, number of ventrals, or number of subcaudals. The largest specimen was a male (NK 982, referred specimen) and had a snout-vent length of 763 mm and tail length of 59 mm; the largest female (NK 636) had a snout-vent length of 618 mm and tail length of 36 mm. The tail is 6.8–8.5% (7.5 ± 0.5, 21) as long as the body in males and 5.8–8.2% (7.3 ± 0.6, 19) as long in females. The head accounts for 2.0–2.5% of snout-vent length in both males (2.2 ± 0.1, 21) and females (2.1 ± 0.7, 17). Ventrals are separated from the second pair of chinshields by 3–5 (4 ± 1, 40) gulars and preventrals and range from 209–220 (215 ± 3, 21) in males and from 208–221 (216 ± 3, 19) in females. Nearly half of all specimens (45%, 40) had 1–20 (2 ± 4) entire subcaudals; subcaudals ranged from 22–26 (24 ± 1, 40) in males and 18–27 (23 ± 2, 40) in females.

*Micrurus serranus* has 10–14 (11.8 ± 1.1, 40) complete triads on the body.

Usually (63%, 40), one and one-third triad is present on the tail and the tip of the tail is black. Less commonly, one (18%, 40), one and two-thirds (16%, 40), or two-thirds (one specimen, 2.5%, 40) triad is present on the tail. The first triad is always complete and is separated from the parietals by 1–5.5 (3.1 ± 1.0, 40) dorsals. In the midbody triad, the red ring extends for 2.5–10.5 (5.5 ± 1.6, 40) dorsals, the first black ring extends for 2–5 (2.9 ± 0.5, 40) dorsals, the first white ring extends for 1.5–3.5 (2.3 ± 0.4, 40) dorsals, and the middle black ring extends for 2–4.5 (3.4 ± 0.7, 40) dorsals. Usually, the red ring is as long as or longer than the middle black ring (number of dorsals in red ring/dorsals in middle black ring = 0.83–5.25, 1.70 ± 0.81, 40). A single specimen (UTA 34561) had the red ring slightly shorter (2.5 dorsals) than the middle black ring (3 dorsals). The first and last black rings of the triads are usually (87.5%, 40) the same size as or shorter than the middle ring (number of dorsals in first black ring/dorsals in middle black ring = 0.5–1.7, 0.87 ± 0.23, 40) and usually (except in UTA 34562) longer than the white rings. Similarly, the white rings are almost always (NK 1472 being the only exception) shorter than the middle black ring (number of dorsals in first white ring/dorsals in middle black ring = 0.4–1.2, 0.68 ± 0.19, 40).

All specimens have the distinctive pale-yellow (white in preservative) band with black-edged scales across the prefrontals. The parietals may be from one-fourth to nearly completely black. The anterior portion of each parietal is always black; generally the apices are black, but they may be immaculate or the red portions of the parietals may have irregular black blotches in them. The anterior chin (mental, anterior infralabials, chinshields) always bears some pigment (minimally the mental and anteriormost infralabials have black blotches or are entirely black), and most specimens were classified as having moderate (65%, 40) to heavy (25%, 40) pigmentation on the anterior chin. Frequently, the pale yellow band on the snout extends across the infralabials and chinshields (i.e, the chin may be black and red or have some pale yellow pigment). The posterior infralabials, posterior chinshields, gulars, and preventrals are usually red. Ventrally, the white rings are shortest and the black rings frequently interrupt the white ring. Red rings are almost always immaculate ventrally. Dorsally, the amount of black in the red rings appears to vary continuously with some specimens (e.g., NK 1722) having nearly immaculate red rings and others (e.g., NK 1323) having nearly every red scale in the rings with a black apex. The amount of black in the white rings is always noticeably greater than in the red rings, and the scales of the white rings always have black apices.

*Etymology*.—The specific epithet *serranus* is an adjective derived from the Spanish adjective *serrano*, meaning highland and refers to the species' restricted range at high elevations in intermontane valleys of Santa Cruz and Cochabamba, Bolivia.

*Natural History*.—Perhaps the most notable characteristic of *Micrurus serranus* is the apparently high proportion of males in the sample: they were ten times more common than females (all adult females were included in the type series). Parker and Plummer (1987) recently reviewed sex ratios in snakes and found that male-biased sex ratios at birth are rare and are documented in only four species. However, male snakes often predominate in samples during periods of high sexual activity. Few specimens in the type series or referred material were collected by us, and more research is required to identify the cause of this skewed sex ratio.

Most specimens of *Micrurus serranus* were heavily infested with mites. NK 1546 was heavily damaged when collected, and we note the presence of the tail of an unidentified *Leptotyphlops* protruding from its belly. NK 1510 was found eating a specimen of *Amphisbaena cegei*. Specimens were encountered throughout the year, although most specimens were collected in December, January, and March, near the beginning and end of the rainy season. In 1991, Harvey found two specimens (UTA 34561–62) on the road after a heavy rain.

Red, black and white banding on the head and neck of the sympatric elapomorphine *Apostolepis multicincta* resembles the pattern on the head of *Micrurus serranus*, and these two venomous species may be part of a Müllerian mimicry system (Harvey, 1999).

*Distribution.*—*Micrurus serranus* appears to be endemic to the intermontane valleys of Santa Cruz and Cochabamba where it occurs at elevations between 1200 and 2150 m. The vast majority of specimens have been collected from the cantons of Mataral and Pampagrande in Florida province, Santa Cruz. The species' existence in Cochabamba is documented by a photograph in Campbell and Lamar (1989) of a specimen from "Aquiles" (= Aiquile, canton Aiquile, Campero province), 2150 m.

The vegetation of the intermontane valleys of Santa Cruz bears a strong resemblance to that of the Gran Chaco (Navarro, 1994). The type locality is characterized by sandy soils with scattered rock outcrops. At a meteorological station in Mairana (1350 m), average annual temperature is 20.9°C and average annual precipitation 575.4 mm. Much of the native vegetation at collecting sites has been altered by agricultural practices.

*Remarks.*—Harvey (1999) discussed the endemic herpetofauna of intermontane vallies of central Bolivia and noted the existence of apparent pairs of sister species with one species occuring in the Andean valleys and another in the Gran Chaco. If the pattern holds for the new species, we predict that its evolutionary affinities lie with the *Micrurus frontalis* complex. However, the new species appears to be more similar to distantly allopatric species such as *M. brasiliensis, M. diana*, and *M. frontalis* than to the Chacoan species *M. pyrrhocryptus*.

### *Micrurus spixii* Wagler
(Fig. 8B, 8D)

*Micrurus Spixii* Wagler, 1824:48. HOLOTYPE male, Rio Solimões, Amazonas, Brazil (ZSMH 209/0).
*Elaps Spixii* (Wagler): Kaup, 1825:593.
*Coluber Marcgravii* (Wied-Neuwied): Fitzinger, 1826:901.
*Elaps Marcgravii* (Wied-Neuwied): Fitzinger, 1826:901; Wagler, 1830:193.
*Elaps corallinus* (Merrem): Schlegel, 1837 (in part); Jan, 1859:275; Jan, 1863*a*:112.
*Elaps spixii* (Wagler): Boulenger, 1896:427 (in part).
*Elaps ehrhardti* Müller, 1926:198. HOLOTYPE female, "Manacapurú am Solimoëns, Brasilien" (=Manacapurú, Rio Solimões, Brazil; ZSM 140/1925) [Amaral (1930*a*:53) mistakenly thought this name was synonymous with *Micrurus lemniscatus*].
*Micrurus spixii* (Wagler): Amaral, 1930*b*:112; Amaral, 1930*c*:232; Schmidt, 1936:198 (in part); Amaral, 1948*b*:159; Hoogmoed, 1979:277; Vanzolini, 1986:24; Fugler, 1986:58 (in part); Fugler and Cabot, 1995:60 (in part).
*Micrurus spixi spixi* (Wagler): Schmidt, 1953*b*:175; Golay et al., 1993:181.
*Micrurus spixi martiusi* Schmidt, 1953*b*:175. HOLOTYPE male, "Santarem, Pará, Brazil" (MCZ 2612). Golay et al., 1993:181 [**new synonymy**, see remarks under *Micrurus obscurus*].
*Micrurus spixii martiusi* (Schmidt): Roze, 1967:42; Roze, 1970:218; Hoge and Romano, 1973:129; Cunha and Nascimento, 1982:21; Roux-Esteve, 1983:89; Roze, 1983:335; Cunha et al., 1985:71; Campbell and Lamar, 1989:146; Roze, 1996:216.
*Micrurus spixii spixii* (Wagler): Roze, 1967:42; Roze, 1970:217; Hoge and Romano, 1973:129; Hoogmoed and Gruber, 1983:334; Roze, 1983:334. Nascimento et al., 1988:56; Campbell and Lamar, 1989:146; Roze and Jorge da Silva, 1990:174; Jorge da Silva, 1993:73; Roze, 1996:215.

*Diagnosis.*—(1) Dorsal pattern of yellow, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) first triad incomplete: one black ring on neck, its anterior margin nearly vertical; (7) dorsal scales of head (including parietals) black with light edges; (8) scales in yellow rings with heavier black apices than scales in red rings; (9) black rings about as long dorsally as ventrally, complete except for black ring straddling the vent; (10) mental usually immaculate, some black edging of more posterior scales on underside of head; (11) 5.33–7.67 (4–9 in specimens from outside Bolivia, Roze, 1996) triads on body and 0.67–1.33 triad on tail.

*Description.*—(Based on 4 males and 3 females). *Micrurus spixii* is a large species, three of our seven specimens exceed one meter, NK 60 being the largest at 1233 mm. The tail is 5.8–7.2% (6.4 ± 0.8, 3) as long as snout-vent length in females and 4.9–6.3% (5.5 ± 0.6, 4) as long in males. Head length accounts for 2.1–2.6% (2.4 ± 0.3, 3) of snout-vent length in females and 2.1–2.4% (2.2 ± 0.1, 4) in males. The distance from the anterior border of the eye to the center of the nostril accounts for 15–22% (19 ± 3, 6) of head-length.

In our sample, cephalic squamation exhibits little variation. All specimens have 2/2 postoculars, 1–1/1–1 temporals, and 7/7 suprlabials and infralabials with supralabials 3–4 entering the orbit. AMNH 22277 has two preoculars on one side, all other specimens have single preoculars. The prefrontals do not contact the supralabials. The supraoculars are 71–86% (79 ± 6, 7) as wide as the frontal. The first three (50% of the time, 7) or the first four infralabials contact the first pair of chinshields so that the third and fourth or just the fourth contact the second. Three to five (3.9 ± 0.7, 7) gulars and preventrals separate the chinshields from the 214–221 (218 ± 4, 3) ventrals and 21–22 (21.3 ± 0.6, 3) subcaudals in females and 213–221 (217 ± 4, 4) ventrals and 19–24 (21.5 ± 2.4, 4) subcaudals in males.

The dorsal head scales of this species are mostly black with red and yellow borders. At least, the first five supralabials bear black posterior edges. The infralabials are invariably patterned, usually with black blotches on the third and fourth infralabial. The mental is immaculate or blotched. The nuchal ring extends for two to three vertebrals behind the parietals and extends ventrally as a complete gular band in all specimens except USNM 280426.

In Bolivia, this species has 5.33–7.67 (6.76 ± 0.81, 7) triads on the body and 0.67–1.33 triads on the tail. Not included in these counts is the incomplete triad (one-third) on the neck. Ventrally, the black rings are as long as or longer than they are dorsally. Where they traverse the vent, black rings may be incomplete ventrally. The first black ring on the neck does not project forward and has a near-vertical anterior margin. The red rings are immaculate or have reduced black apices, and the yellow rings have heavy black apices.

At midbody, the red ring extends for 4–11.5 (8.2 ± 3.0, 7), the exterior black ring for 3–5 (4.0 ± 0.7, 7), the yellow ring for 4–8 (5.3 ± 1.3, 7), and the middle black ring for 2–4.5 (3.4 ± 0.9, 7) vertebrals. Relative lengths of the rings overlap, although the red ring is usually longest followed in size by the yellow ring, then the exterior black rings. The exterior black rings are 100–133% (120 ± 18, 7) and the yellow rings 122–200% (160 ± 37, 7) as long as the middle black ring. The middle black ring is 26–75% (46 ± 17, 7) as long as the red ring.

*Distribution and Comparative Material.*—**BOLIVIA. BENI. Vaca Diez:** Riberalta (UMMZ 63820), Tumi Chucua (USNM 280426), Guayaramerín (USNM 280976). **Unknown:** "Rio Itenez, Puerto Capitan Vasquez," (AMNH 113603). **SANTA CRUZ. Velasco:** Santa Cruz: "Huanchaca I", Mesa of the Serranía de Huanchaca (NK 604), "Arriba de Lago Caiman, la meseta de Parque Noel Kempff" (NK 1310).

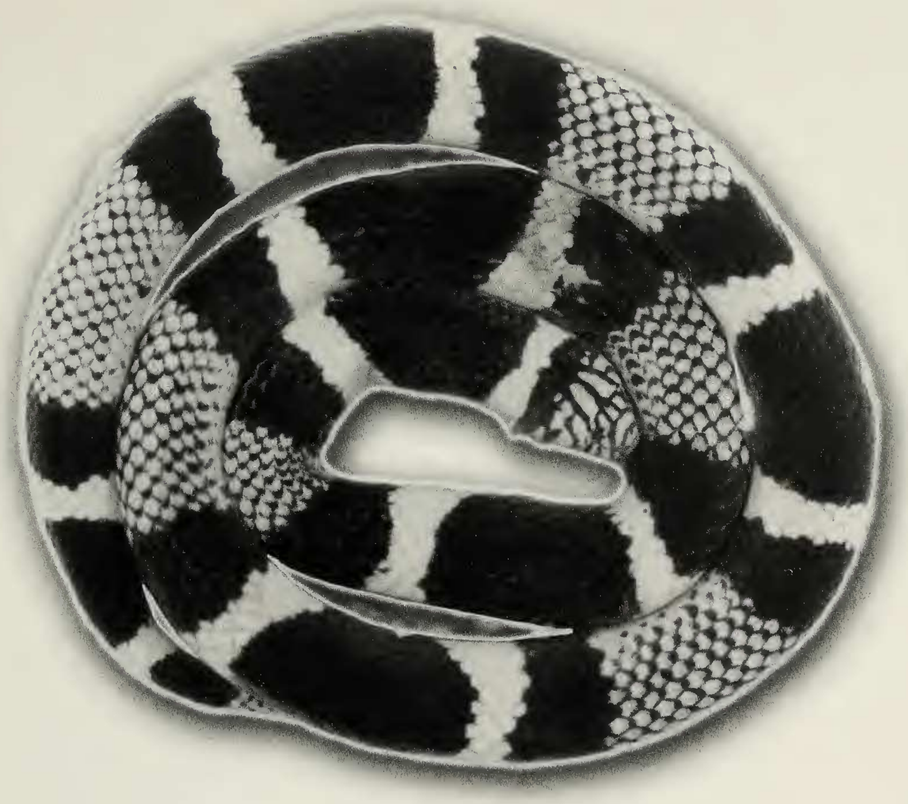

Fig. 14.—*Micrurus surinamensis* (KU 183492 F, SVL 664 mm) from 15 km SW of Villa Tunari, Chapare, Cochabamba.

**BRAZIL. PARA:** USNM 267833. **BRAZIL. BAHIA:** AMNH 22277.

## *Micrurus surinamensis* Cuvier
(Fig. 14)

*Elaps surinamensis* Cuvier, 1817:84. SYNTYPES a male (MNHN 3926) and a female (MNHN 3925) [Roux-Esteve (1983) points out that MNHN 3924 is the specimen illustrated by Jan and Sordelli, however this specimen is not a type specimen. Schmidt (1952:29) designated MNHN "4629" (=3926), as a lectotype.]. Cope, 1876:182; Boulenger, 1896:414.

*Micrurus surinamensis* (Cuvier): Amaral, 1925:17; Amaral, 1948*a*:38; Amaral, 1948*b*:159; Fugler, 1986:58; Fugler and Cabot, 1995:60.

*Micrurus surinamensis surinamensis* (Cuvier): Schmidt, 1952:29; 1955:349; Roze, 1955:491; Peters, 1960:532; Roze, 1967:49; Brongersma, 1967:73, 75; Roze, 1970:219; Hoge and Romano, 1973: 130; Cunha and Nascimento, 1982:23; Carrillo de Espinoza, 1983:45; Dixon and Soini, 1986: 146; Vanzolini, 1986:24; Campbell and Lamar, 1989:152; Golay et al., 1993:183; Jorge da Silva, 1993:74; Carrillo de Espinoza and Icochea, 1995:19; David and Ineich, 1999:155.

*Diagnosis.*—(1) Dorsal pattern of white, red, and black triads; (2) hemipenis relatively short; tail 10–14% of snout-vent length; (3) one supralabial entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) first triad complete (7) first black ring short and overlapping or closely approximating parietals; (8) dorsal surface of head red with all scales edged in black; (9) extent of black pigment in red and white rings variable; (10) white rings longest ventrally, never constricted or broken ventrally by black rings; (11) scales of chin red with black edges; (12) 5.33–6.67 triads on body, 1–2 triads on tail.

*Description.*—(Based on 8 females, 7 males, and 2 unsexed specimens). Although one of the most recognizable coralsnakes, relatively few Bolivian specimens have been examined previously. In his review of this species, Schmidt (1952) had access to only two Bolivian specimens, both male. In our sample, extreme total lengths are 1338 mm (a female, NK 723) and 282 mm (a male, CBF 675). The tail is 10–13% (12.1 ± 2.0, 7) as long as the body in females and 13–14% (13.7 ± 0.4, 6) as long in males. Head length accounts for 2.4–3.9% (3.1 ± 0.6, 5) of snout-vent length in females and 2.8–4.3% (3.4 ± 0.6, 6) in males. Distance from the anterior border of the orbit to the center of the nostril is 17.5–24.6% (22.2 ± 2.9, 13) of head length.

As for populations elsewhere, Bolivian specimens have a narrow frontal which is 73–92% (83 ± 7, 11) as wide as the supraocular. KU 183492 has only 6/6 supralabial and supralabial 3/3 enters the orbit. In all other specimens, the fourth supralabial enters the orbit and seven supralabials are present. The prefrontal does not contact the supralabials. Most specimens had two postoculars; one is present on both sides in CBF 949 and on one side only in CBF 868 (9.4%). The Bolivian specimens have 1+1 (81%, 18) or 1+2 (19%, 18) temporals. All specimens had 7/7 infralabials, the first three (9%, 19) or four (91%, 19) contacting the first pair of chinshields. The mental does not contact the chinshields. Three to six (4 ± 1, 17) gulars and preventrals separate the second pair of chinshields from 168–182 (179 ± 5, 8) ventrals and 28–34 (30 ± 2, 7) subcaudals in females and 165–174 (169 ± 3, 7) ventrals and 28–36 (34 ± 3, 7) subcaudals in males. Forty-three percent (15) of the specimens had 2–5 entire subcaudals located proximally on the tail.

In our sample, the first black ring is short and usually covers the posterior tips of the parietals and one to two vertebrals. In CBF 868, the first black ring does not involve the parietals: their tips and 1/2 of the first vertebral are red. Based on 17 males and 13 females, Hoge (1958) concluded that the first ring of the neck triad is complete in males (i.e., a complete gular ring is present) and incomplete in females. However, sexual dimorphism in this character was not evident in our sample. The gular ring includes gulars and the apices of the posterior chinshields. In males and females, the gular ring usually is complete, but in both sexes the scales within the ring are approximately one-half red with black edges. In only three males (e.g., NK 2033), the scales within the ring are entirely black. The second black ring is incomplete in 36% of the specimens and is not sexually dimorphic. In addition to the neck triad, females in our sample have five and two-thirds to six and one-third triads on the body and one to one and two-thirds on the tail. In addition to the neck triad, males have 5.33 to 6.67 triads on the body and one and one-third to two triads on the tail. The rings of this species are sharply angled so that the black rings are longest dorsally and the white rings are longest ventrally. CBF 1763 has an anomolous pattern with black rings that are incomplete ventrally and appear as black circles surrounded by white.

At midbody, the red rings are 6–12 (7.9 ± 2.0, 15), the exterior black rings are 2–4 (3.1 ± 0.5, 15), the white rings are 1–2 (1.6 ± 0.4, 15), and the middle black rings are 7–10.5 (8.2 ± 1.0, 15) vertebrals long. Based primarily on material from outside Bolivia, this species has been characterized as having red rings usually longer than middle black rings (Roze, 1996). However, in our sample, this is true for only five specimens. The middle black ring is 67–154% (111 ± 28, 15) as long as the red ring. The middle black ring is always longer than the exterior black rings and the white rings: the exterior black ring is 33–47% (39 ± 8, 15) as long and the white ring is 11–31% (20 ± 6, 15) as long as the middle black ring.

*Distribution.*—**BOLIVIA. BENI. Gral. José Ballivián:** Estación Biologica del Beni (CBF 1175), "proximo al Estación Biologica del Beni," (CBF 1763), Bosque Chimanes (CBF 1123). **Moxos:** "carreterra entre el Río Cuberene y el Río Museruna (CBF 1534), San Ignacio de Moxos (NK 2033). **Vaca Diez:** "Rio Marmoré, Isla Nicolas Suaréz (between Guayaramerin, Bolivia and Guajará-Mirim, Brazil)" (AMNH 113604), Río Marmoré, Guayaramerín (AMNH 113605) **Yacuma:** Estación Biologica del Beni, Campamento El Trapiche (CBF 948). **COCHABAMBA: Chapare.** 15 km SW Villa Tunari, 660 m (KU 183492). **PANDO. Manuripi:** 8 km SW of Santa Rosa (CBF 868). **SANTA CRUZ. Andrés Ibáñez:** Santa Cruz de la Sierra (CM 2795), Terevinto (NK 484), Potrerillo de Guendá (NK 723, NK 1418). **Ichilo:** Buena Vista (NK 838), (Parque Nacional Amboró, 17°24′12″S, 64°14′23″W (NK 1324). **Velasco:** Los Fierros, Parque Nacional "Noel Kempff Mercado" (NK 279). **Unknown:** "112 km N Santa Cruz de la Sierra, ca 1200 ft" (AMNH 119936).

Not examined: BMNH 27-8-1-218 (from Buena Vista, Ichilo province, see Schmidt, 1952).

## DISCUSSION

The ranges of three coralsnakes approach Bolivia's borders, and each may occur within the country. *Micrurus albicinctus, M. mipartitus*, and *M. paraensis* occur in Rondônia (Vanzolini, 1986; Nascimento et al., 1988; Jorge da Silva, 1993). Campbell and Lamar (1989) predict that *M. langsdorffi* probably occurs in Bolivia, however these authors are referring to *M. albicinctus*. Campbell and Lamar (1989) agreed with Cunha and Nascimento's (1982) synonymization of *M. albicinctus* with *M. ornatissimus*, which they considered to be a subspecies of *M. langsdorffi*. Other species of the *M. frontalis* complex may be discovered in Bolivia. Recent collections in the vicinity of the Serranía de Huanchaca have failed to produce a species of this complex other than *M. diana*. In Chiquitos province, *M. diana* occurs in sympatry with *M. pyrrhocryptus*, however the Serranía de Huanchaca lies between the ranges of *M. pyrrhocryptus* and *M. frontalis*. Several Brazilian species such as *Hoplocercus spinosus* just enter the country in this area (Harvey, 1998), and the same may be true for *M. frontalis*: its closest locality is in Mato Grosso (Jorge da Silva and Sites, 1999). *Micrurus baliocoryphus* occurs in the Argentine Mesopotamia and approaches Bolivia in the Paraguayan province of Presidente Hayes (Jorge da Silva and Sites, 1999), however the closest localities are still almost 500 km from the Bolivian border.

A specimen identified as *Micrurus corallinus* (CM 261) by Griffin (1916) and Amaral (1926*a*) was collected by T. LeBoutelier from "Sierras of Bolivia." The specimen was missing from the collection during an inventory in August 22, 1960, and the specimen has not yet been found. Griffin (1916) reported that LeBoutelier rarely provided accurate locality data; many specimens he collected bear no data other than from "South America." Reporting on the specimen at the Carnegie Museum, he gave "LeBoutelier Collection, South America," apparently placing little faith that the specimens actually came from Bolivia. Amaral (1926*a*) reported this species from Bolivia. The specimen was a female 597 mm total length (tail 83 mm) with "1,1" temporals, a divided anal, 200 ventrals, 43 divided subcaudals, 16 black rings on the body, and 6 black rings on the tail (Amaral, 1926*a*; Griffin, 1916). However, both authors' concept of *M. corallinus* was flawed; in a later publication, Amaral (1930*a*) thought that *Elaps balzani* Boulenger (= *M. annellatus*) was *M. corallinus corallinus*. Currently, *Micrurus corallinus* is thought to be restricted to southeastern and central Brazil, eastern Paraguay, and northeastern Misiones, Argentina (Campbell and Lamar, 1989; Roze, 1996).

Fugler (1986) included *Micrurus ibiboboca* (Merrem) in the Bolivian fauna citing Boulenger (1898) and Werner (1901). In his literature cited, Fugler lists two publications of Boulenger for 1898. Neither publication contains a reference to *M. ibiboboca*. One of these publications reports on a collection from the upper Río Paraguay (Boulenger, 1898*b*) and contains a specimen of the *Micrurus frontalis* complex. However, Fugler clearly was referring to Boulenger's report on Balzan's collection (Boulenger, 1898*a*), where Boulenger lists "*Elaps marcgravii*, Wied." from Reyes and Santa Ana de Movimas, Beni. Fugler is correct that *E. marcgravii* is a synonym of *M. ibiboboca*, however, Boulenger applied the name to *M. lemniscatus* as well (Schmidt, 1957). Other authors have applied the name to *M. spixii* and *M. obscurus*, however Boulenger used Peters' junior synonym *Elaps heterozonus* to refer to *M. obscurus*. *Micrurus ibiboboca* is restricted to eastern Brazil and the western limit of its range is far from the Bolivian border.

Schmidt (1936) pointed out the "difficult problems of distribution" posed by a specimen of *Micrurus tschudii* said to be from Bolivia in the Museum National d'Histoire Naturelle in Paris, whereas all other specimens of *M. tschudii* are from coastal Peru. He chose not to include Bolivia in the distribution of this species. Less skeptically, Roze (1967, 1983, 1996) reports that the subspecies *M. tschudii tschudii* occurs on the "Pacific slopes from southern Ecuador to southern Peru and probably northwestern Bolivia" (Roze, 1983). Without comment, Bolivia was included in the distribution of this species by Peters and Orejas-Miranda (1970) and repeated by Fugler and Cabot (1995). Campbell and Lamar (1989) cautioned "the postulated occurrence of *M. tschudii* in Bolivia is difficult to explain, as the Andes constitute a formidable barrier to dispersal in this region."

The specimen of *Micrurus tschudii* collected by Wiener and labelled "Bolivia" may well have come from northern Chile or southwestern Peru. These coastal regions were inside the border of Bolivia prior to Bolivia's war with these countries between 1879 and 1884. Nonetheless, the most southern localities for this species are in Lima Department (Carrillo de Espinoza and Icochea, 1995). Schmidt (1936) remarked that the specimen said to come from Bolivia more closely agreed with his diagnosis of *Micrurus tschudii olssoni* except that it lacks a mottled snout.

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## LITERATURE CITED

ABALOS, J. W. 1961. Distribución y densidad de las serpientes venenosas de Santiago del Estero. Acta Krausi Cuaderno del Instituto Nacional de Microbiologia (Buenos Aires), 3:67–70.

ABALOS, J. W., AND C. C. MISCHIS. 1975. Elenco sistemático de los ofidios Argentinos. Boletín de la Academia Nacional de Ciencias (Cordoba), 51:55–76.

ABALOS, J. W., AND R. NADER. 1962. La coral *Micrurus lemniscatus frontalis* de Santiago del Estero. Anales del Instituto Nacional de Microbiologia (Buenos Aires), 1:83–94.

ABALOS, J. W., E. C. BÁEZ, AND R. NADER. 1964. Serpientes de Santiago del Estero. Acta Zoologica Lilloana, 20:211–283.

ABUYS, A. 1987. The snakes of Surinam, part XVIII: family Elapidae, subfamily Micrurinae. Litteratura Serpentium, 7:221–242.

AMARAL, A. DO. 1925. South American snakes in the collection of the United States National Museum. Proceedings of the United States National Museum, 67:1–30.

———. 1926*a*. Três subespecies novas de *Micrurus corallinus* (WIED): *M. corallinus corallinus, M. corallinus riesei e M. corallinus dumerilii.* Revista do Museu Paulista, 15:13–25.

———. 1926*b*. Studies of Neotropical Ophidia. II. On *Micrurus mipartitus* and allied forms. Proceedings of the New England Zoological Club, 9:61–66.

———. 1926*c*. Da invalidez de especie de colubrideo elapineo *Micrurus ibiboboca* (Merrem) e redescripção de *M. lemniscatus* (L.). Revista do Museu Paulista, 15:29–40.

———. 1930*a* (dated 1929). Estudos sobre ophidios Neotropicos. XVII. Valor sistematico de varias formas de ophidios neotropicos. Memórias do Instituto Butantan, 4:1–68.

———. 1930*b* (dated 1929). Contribuição ao conhecimento dos ophidios do Brasil. IV. Lista remissiva dos ophidios do Brasil. Memórias do Instituto Butantan, 4:69–125.

———. 1930*c* (dated 1929). Estudos sobre ophidios neotropicos. XVIII. Lista remissiva dos ophidios da região neotropica. Memórias do Instituto Butantan, 4:129–271.

———. 1931. Studies of Neotropical Ophidia XXVI. Ophidia of Colombia. Bulletin of the Antivenin Institute of America, 4:89–94.

———. 1944. Notas sobre a ofiologia neotrópica e brasílica XI. Subespécies de *Micrurus lemniscatus* (L.) e suas afinidades com *M. frontalis* (Dm. & Bibr.). Papéis Avulsos do Departamento de Zoologia, 5:83–93.

———. 1948*a*. Ofídios de Mato Grosso. Comissão de Linhas telegráficas estratégica de Mato Grosso ao Amazonas, 84:1–43.

———. 1948*b*. Ofídios do Pará. Boletim do Museu Paraense Emílio Goeldii, Zoologia, 10:149–159.

———. 1977. Serpentes do Brasil: Iconografia Colorida. Universidade de São Paulo, São Paulo, Brazil.

AVISE, J. C., AND R. M. BALL, JR. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Survey in Evolutionary Biology, 7:45–67.

BARBOUR, T., AND G. K. NOBLE. 1920. Amphibians and reptiles from southern Peru collected by the Peruvian expedition of 1914–1915 under the auspices of Yale University and the National Geographic Society. Proceedings of the United States National Museum, 58:609–620.

BARRIO, A, AND M. E. MIRANDA. 1967 (dated 1966). Estudio comparativo morfológico e inmunológico entre las diferentes entidades del género *Micrurus* Wagler (Ophidia, Elapidae) de la Argentina. Memórias do Instituto Butantan, 33:869–880.

BEEBE, W. 1919. The higher vertebrates of British Guiana. List of Amphibia and Mammalia. Zoologica, 2:205–216.

———. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. Zoologica, 31:11–52.

BERG, C. 1898. Contribuciones al conocimiento de la fauna erpetológica argentina. Anales del Museo Nacional de Buenos Aires, 6:1–35.

BOULENGER, G. A. 1896. Catalogue of the Snakes in the British Museum (Natural History). Volume 3. British Museum (Natural History), London, United Kingdom.

———. 1898*a*. A list of the reptiles and batrachians collected by the late prof. L. Balzan in Bolivia. Annali dell Museo Civico di Storia Naturale di Genova, ser. 2, 19:128–133.

———. 1898*b*. A list of reptiles, batrachians, and fishes collected by Cav. Guido Boggiani in the northern Chaco. Annali dell Museo Civico di Storia Naturale di Genova, ser. 2, 19:125–127.

———. 1902*a*. List of the fishes, batrachians, and reptiles collected by the late Mr. P. O. Simons in the provinces of Mendoza and Cordova, Argentina. Annals and Magazine of Natural History, ser. 7, 9:336–339.

———. 1902*b*. Description of new batrachians and reptiles from the Andes of Peru and Bolivia. Annals and Magazine of Natural History, ser. 7, 10:394–402.

———. 1905. Descriptions of new snakes in the collection of the British Museum. Annals and Magazine of Natural History, ser. 7, 15:453–456.

BRONGERSMA, L. D. 1967 (dated 1966). Poisonous snakes of Surinam. Memórias do Instituto Butantan, 33:73–79.

BUCHER, E. H. 1980. Ecología de la fauna chaqueña. Una revision. ECOSUR, 7:111–159.

BURGER, W. L. 1955. A new subspecies of the coralsnake *Micrurus lemniscatus*, from Venezuela, British Guiana, and Trinidad; and a key for the identification of associated species of coralsnakes. Boletin del Museo de Ciencias Naturales (Caracas), 1:35–51.

CAMPBELL, J. A. 2000. A new species of venomous coralsnake (Serpentes: Elapidae) from high desert in Puebla, Mexico. Proceedings of the Biological Society of Washington, 113:291–297.

CAMPBELL, J. A., AND W. W. LAMAR. 1989. The Venomous Reptiles of Latin America. Cornell University Press, Ithaca, New York.

CAPOCACCIA, L. 1961. Catalogo dei tipi de rettili del Museo Civico di Storia Naturale di Genova. Annali dell Museo Civico di Storia Naturale di Genova, 72:86–111.

CARRILLO DE ESPINOZA, N. 1983. Contribución al conocimiento de las serpientes venenosas del Perú de las familias Viperidae, Elapidae, e Hydrophiidae. Publicaciones del Museo de Historia Natural "Javier Prado," 30:1–55.

CARRILLO DE ESPINOZA, N., AND J. ICOCHEA. 1995. Lista taxonomica preliminar de los reptiles vivientes del Peru. Publicaciones del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, 49:1–27.

COPE, E. D. 1859. Catalogue of the venomous serpents in the museum of the Academy of Natural Sciences of Philadelphia, with notes on the families, genera, and species. Proceedings of the Academy of Natural Sciences of Philadelphia, 1859:332–347.

———. 1862. Catalogues of the reptiles obtained during the explorations of the Parana, Paraguay, Vermejo and Uraguay rivers by Capt. Thos. J. Page, U. S. N.; and of those procured by Lieut. N. Michler, U. S. Top. Eng., commander of the expedition conducting the survey of the Atrato river. Proceedings of the Academy of Natural Sciences Philadelphia, 1862:346–359.

———. 1876. Report on the reptiles brought by professor James Orton from the middle and upper Amazon, and western Peru. Journal of the Academy of Natural Sciences of Philadelphia, 8:159–87.

CRUZ, F. B., M. G. PEROTTI, AND L. E. FITZGERALD. 1992. Lista de anfibios y reptiles colectados en una localidad del chaco salteño. Acta Zoologica Lilloana, 42:101–107.

CUNHA, O. R. DA, AND F. P. DO NASCIMENTO. 1982. Ofídios da Amazônia. XIV. As espécies de *Micrurus, Bothrops, Lachesis, e Crotalus* do sul do Pará e oeste do Maranhão, incluindo áreas de cerrado deste estado. (Ophidia: Elapidae e Viperidae). Boletim do Museu Paraense Emílio Goeldi, Zoologia, 112:1–58.

CUNHA, O. R. DA, F. P. DO NASCIMENTO, AND T. C. S. DE ÁVILA-PIRES. 1985. Os Répteis da área de Carajás, Pará, Brasil (Testudines e Squamata). I. Publicação Avulsas do Museu Paraense Emílio Goeldi, 40:9–94.

CUVIER, G. L. C. F. D. 1817. Le Regne Animal. Paris, France, 8:I–xviii, 1–532.

DAVID, P., AND I. INEICH. 1999. Les serpents venimeux du monde: systématique et repartition. Dumerilia, 3:3–499.

DI-BERNARDO, M., M. BORGES-MARTINS, AND L. H. CAPPELLARI. 2001. Geographic Distribution: *Micrurus lemniscatus*. Herpetological Review, 32:60.

DIXON, J. R., AND P. SOINI. 1986. The Reptiles of the Upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee.

DOWLING, H. G. 1951. A proposed standard system of counting ventrals in snakes. British Journal of Herpetology, 1:97–99.

DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. University of Kansas Museum of Natural History Miscellaneous Publication, 65:1–352.

———. 1979. The herpetofauna of the Andes: patterns of distribution, origin, differentiation and present communities. Pp. 371–459, *in* The South American Herpetofauna: Its Origin, Evolution, and Dispersal (W. E. Duellman, ed.). Monograph of the Museum of Natural History, The University of Kansas, No. 7.

FITZINGER, L. I. 1826. Kritische Bemerkungen über J. Waglers Schlangenwerk. Isis (Oken), 1826: 881–909.

FROST, D. R., AND D. M. HILLIS. 1990. Species in concept and practice: herpetological applications. Herpetologica, 46:87–104.

FUGLER, C. M. 1986. Una lista preliminar de las serpientes de Bolivia. Ecología en Bolivia (La Paz), 8:45–72.

FUGLER, C. M., AND J. CABOT. 1995. Herpetologica Boliviana: una lista comentada de las serpientes de Bolivia con datos sobre su distribución. Ecología en Bolivia (La Paz), 1995:40–87.

GANS, C. 1960. Notes on a herpetological collecting trip through the southeastern lowlands of Bolivia. Annals of the Carnegie Museum, 35:283–255.

GOLAY, P. 1985. Elapsoidea. Checklist and Keys to the Terrestrial Proteroglyphs of the World. Gilbert Rey, Geneva, Switzerland.

GOLAY, P., H. M. SMITH, D. G. BROADLEY, J. R. DIXON, C. MCCARTHY, J.-C. RAGE, B. SCHÄTTI, AND M. TORIBA. 1993. Endoglyphs and Other Major Venomous Snakes of the World. A Checklist. Azemiops, Switzerland.

GONZALES A., L. 1998. La herpetofauna del Izozog. Ecología en Bolivia (La Paz), 1998:45–52.

GRIFFIN, L. E. 1916. A catalog of the ophidia from South America at present (June, 1916) contained in the Carnegie Museum with description of some new species. Memoirs of Carnegie Museum, 7:163–228.

GUEDES, A. G. 2000. Geographic distribution: *Micrurus frontifasciatus*. Herpetological Review, 31: 225.

GÜNTHER, A. 1859. On the genus *Elaps* of Wagler. Proceedings of the Zoological Society of London, 1859:79–89.

———. 1861. Account of the reptiles sent by Dr. Wucherer from Bahia. Proceedings of the Zoological Society of London, 1861:12–18.

HARVEY, M. B. 1998. Reptiles and amphibians of Parque Nacional Noel Kempff Mercado. Pp. 144–166, 348–355, *in* A Biological Assessment of Parque Noel Kempff Mercado, Bolivia (T. J. Killeen and T. S. Schulenberg, eds.). Conservation International, Washington, D.C.

———. 1999. Revision of Bolivian *Apostolepis* (Squamata: Colubridae). Copeia, 1999:388–409.

HOGE, A. R. 1957 (dated 1955/6). Uma nova espécie de *Micrurus* (Serp. Elap.) do Brasil. Memórias do Instituto Butantan, 27:67–72.

———. 1958. Tres notas sobre serpentes brasileiras. Papéis Avulsos do Departamento de Zoologia, 13:221–225.

HOGE, A. R., AND A. R. LANCINI. 1960 (dated 1959). Nota sobre *Micrurus surinamensis nattereri* Schmidt e *Micrurus pyrrhocryptus* Cope. Memórias do Instituto Butantan, 29:9–13.

HOGE, A. R., AND S. A. ROMANO. 1966 (dated 1965). *Leptomicrurus* in Brasil (Serpentes-Elapidae). Memórias do Instituto Butantan, 32:1–8.

———. 1972 (dated 1971). *Micrurus hemprichii hemprichii* recorded from Brazil (Serpentes Elapidae). Memórias do Instituto Butantan, 35:107–109.

———. 1973 (dated 1972). Sinopse das serpientes peçonhentas do Brasil. Memórias do Instituto Butantan, 36:109–208.

HOOGMOED, M. S. 1979. The herpetofauna of the Guianan Region. Pp. 241–280, *in* The South American Herpetofauna (W. E. Duellman, ed.). Monograph of the Museum of Natural History, The University of Kansas, No. 7.

HOOGMOED, M. S., AND U. GRUBER. 1983. Spix and Wagler type specimens of reptiles and amphibians in the Natural History Musea [sic] in Munich (Germany) and Leiden (The Netherlands). Spixiana, supplement, 9:319–415.

JAN, G. 1859. Spix' Serpentes Brasiliensis beurteilt nach Autopsie der Originalexemplare und auf die Nomenclatur von Duméril und Bibron zurückgeführt. Archiv für Naturgeschichte, 25:272–275.

———. 1863*a*. Elenco sistematico degli ofidi descritti e disegnati per l'Iconografia Generale. A. Lombardi, Milan, Italy.

———. 1863*b*. Enumerazione sistematica degli ofidi appartenenti al gruppo Coronellidae. Archivo per la Zoologia, l'Anatomia e la Fisiologia (Genova), 21:213–330.

JAN, G., AND F. SORDELLI. 1870–1881. Iconographie Générale des Ophidians. Vol. 3, Livraisons 35–50. Milan, Italy.

JORGE DA SILVA, N, JR. 1993. The snakes from Samuel Hydroelectric Power Plant and vicinity, Rondônia, Brazil. Herpetological Natural History, 1:37–86.

JORGE DA SILVA, N, JR., AND J. W. SITES, JR. 1999. Revision of the *Micrurus frontalis* complex (Serpentes: Elapidae). Herpetological Monographs, 13:142–194.

———. 2001. Phylogeny of South American triad coralsnakes (Elapidae: *Micrurus*) based on molecular characters. Herpetologica, 57:1–22.

KARDONG, K. V. 1980. Evolutionary patterns in advanced snakes. American Zoologist, 20:269–282.

KAUP, J. J. 1825. Einige Bemerkungen zu dem Spixiischen Prachtwerke. Isis (Oken), 16:593.

KILLEEN, T. J., AND T. S. SCHULENBERG. 1998. A Biological Assessment of Parque Nacional Noel Kempff Mercado, Bolivia. RAP Working Papers 10. Conservation International, Washington, D.C.

KORNACKER, P. M. 1999. Checklist and key to the snakes of Venezuela. PaKo-Verlag, Rheinbach, Germany.

LANCINI V., A. R. 1979. Serpientes de Venezuela. Ernesto Armitano, Caracas.

LAURENT, R. F., AND E. M. TERAN. 1981. Lista de los anfibios y reptiles de la provincia de Tucumán. Fundación Miguel Lillo Miscelanea, 71:1–15.

LAVILLA, E. O., F. B. CRUZ, AND G. J. SCROCCHI. 1995. Amphibiens et reptiles de la Station Biologique "Los Colorados" dans la province de Salta, Argentine (2^e partie). Revue francaise d'Aquariologie et Herpetologie, 22:117–128.

LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology. Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia, 1985:802–832.

LEYNARD, G. C., AND E. H. BUCHER. 1999. La fauna de serpientes del chaco sudamericano: diversidad, distribución geográfica y estado de conservación. Academia Nacional de Ciencias Miscelanea, 98:1–46.

LÖNNBERG, E. 1902. On a collection of snakes from north-western Argentina and Bolivia containing new species. The Annals and Magazine of Natural History, 7:457–462.

MIYATA, K. 1982. A check list of the amphibians and reptiles of Ecuador with a bibliography of Ecuadorian herpetology. Smithsonian Herpetological Information Service, 54:1–70.

MÜLLER, VON L. 1926. Neue Reptilien und Batrachier der Zoologischen Sammlung des bayrischen Staates. Zoologischer Anzeiger, 65:193–200.

NASCIMENTO, F. P. DE. 1988. Répteis Squamata de Rondônia e Mato Grosso colectados através do Programa Polonoroeste. Boletim do Museu Paraense Emílio Goeldii, Zoologia, 4:21–66.

NASCIMENTO, F. P. DE., T. C. S. DE AVILA-PIRES, AND O. R. DA CUNHA. 1987. Os répteis da áre de Carajás, Pará, Brasil (Squamata). II. Boletim do Museu Paraense Emílio Goeldii, Zoologia, 3:33–65.

———. 1988. Répteis Squamata de Rondônia e Mato Grosso colectados através do programa Polonoroeste. Boletim do Museu Paraense Emílio Goeldii, Zoologia, 4:21–66.

NAVARRO, G. S. 1994. Avance sobre un modelo intergrado de sectorización biogeográfica de Bolivia. Revista de la Sociedad de Estudios Botanicos (Santa Cruz de la Sierra, Bolivia), 1:40–48.

PARKER, W. S., AND M. V. PLUMMER. 1987. Population ecology. Pp. 253–301, *in* Snakes, Ecology and Evolutionary Biology (R. A. Seigel, J. T. Collins, and S. S. Novak, eds.). MacMillan, New York, New York.

PÉREZ-SANTOS, C, AND A. G. MORENO. 1988. Ofidios de Colombia. Museo Regionale di Sienze Naturali, Torino, Mongrafia 6.

PERACCA, M. G. 1895. Viaggio del dott. Alfredo Borelli nella Repubblica Argentina e nel Paraguay. Bollettino del Musei di Zoologia ed Anatomia comparata della R. Università Torino, 10:1–32.

———. 1897*a*. Intorno ad una piccola raccolta di rettili di Cononacco (Peru orientale). Bollettino del Musei di Zoologia ed Anatomia comparata della R. Università Torino, 12 (284):1–7.

———. 1897*b*. Viaggio del Dott. Alfredo Borelli nel Chaco boliviano e nella Repubblica Argentina. Bollettino del Musei di Zoologia ed Anatomia comparata della R. Università Torino, 12 (274):1–19.

PETERS, J. A. 1960. The snakes of Ecuador. A checklist and key. Bulletin of the Museum of Comparative Zoology at Harvard College, 122:491–541.

PETERS, J. A., AND B. OREJAS-MIRANDA. 1970. Catalogue of the Neotropical Squamata. Part I. Snakes. United States National Museum Bulletin, 297:i–viii, 1–347.

PETERS, W. 1871. Über eine von Hrn. Dr. Robert Abendroth in dem Hochlande von Peru gemachte Sammlung von Amphibien, welche derselbe dem Königl. Monatsberichte der Preussischen Akademie der Wissenschaften zu Berlin, 3:397–404.

———. 1881. Über das Vorkommen schildförmiger Verbreiterungen der Dornfortsätze bei Schlangen und über neue oder weniger bekannte Arten dieser Abtheilung der Reptilien. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1881:49–52.

RIVERO-BLANCO, C., AND J. R. DIXON. 1979. Origin and distribution of the herpetofauna of the dry lowland regions of northern South America. Pp. 281–298, *in* The South American Herpetofauna (W. E. Duellman, ed.). Monograph of the Museum of Natural History, The University of Kansas No. 7.

ROMANO, S. A. R. W. L. 1972 (dated 1971). Notes on *Leptomicrurus* Schmidt. Memórias do Instituto Butantan, 35:111–115.

ROUX-ESTEVE, R. 1983. Les specimens-types du genre *Micrurus* (Elapidae) conserves au Muséum national d'Histoire Naturelle de Paris. Memórias do Instituto Butantan, 46:79–90.

ROZE, J. A. 1955. Revisión de las corales (Serpentes: Elapidae) de Venezuela. Acta Biologica Venezuelica, 1:453–500.

———. 1967. A check list of the New World venomous coralsnakes (Elapidae), with descriptions of new forms. American Museum Novitates, 2287:1–60.

———. 1970. *Micrurus*. Pp. 196–220, *in* Catalogue of the Neotropical Squamata. Part I. Snakes (J. A. Peters and B. Orejas-Miranda, eds.). Smithsonian, Washington, D. C.

———. 1983. New world coralsnakes (Elapidae): a taxonomic and biological summary. Memórias do Instituto Butantan, 1982:305–338.

———. 1994. Notes on taxonomy of venomous coralsnakes (Elapidae) of South America. Bulletin of the Maryland Herpetological Society, 30:177–185.

———. 1996. Coralsnakes of the Americas. Biology, Identification, and Venoms. Krieger, Malabar, Florida.

ROZE, J. A., AND A. BERNAL-CARLO. 1987. Las serpientes corales venenosas del género *Leptomicrurus* (Serpentes, Elapidae) de Suramérica con descripción de una nueva subespecies. Bolletino del Museo Regionale di Sciènze Naturali (Torino), 5:573–608.

ROZE, J. A., AND N. JORGE DA SILVA. 1990. Coralsnakes (Serpentes, Elapidae) from hydroelectric power plant of Samuel, Rondônia, Brazil, with description of a new species. Bulletin of the Maryland Herpetological Society, 26:169–176.

SAVAGE, J. M., AND J. B. SLOWINSKI. 1992. The colouration of the venomous coralsnakes (family Elapidae) and their mimics (families Aniliidae and Colubridae). Zoological Journal of the Linnean Society, 45:235–254.

SAVITZSKY, A. H. 1978. The origin of the New World proteroglyphous snakes and its bearing on the study of venom delivery systems in snakes. Unpublished PhD Dissert., University of Kansas, Lawrence, Kansas.

SCHLEGEL, H. 1837. Essai sur la physionomie des serpens. Partie descriptive. Leide, Arns, and Compagnie, Paris, France.

SCHMIDT, K. P. 1928. Notes on American coralsnakes. Bulletin of the Antivenin Institute of America, 2:63–64.

———. 1936. Preliminary account of coral snakes of South America. Fieldiana, 20:189–203.

———. 1937. The history of *Elaps collaris* Schlegel 1837–1937. Zoological Series of the Field Museum of Natural History, 20:361–364.

———. 1952. The Surinam coralsnake *Micrurus surinamensis*. Fieldiana, 34:25–34.

———. 1953*a*. Hemprich's coralsnake *Micrurus hemprichi*. Fieldiana, 34:165–170.

———. 1953*b*. The Amazonian coralsnake *Micrurus spixii*. Fieldiana, 34:171–180.

———. 1954. The annellated coralsnake *Micrurus annellatus* Peters. Fieldiana, 34:319–325.

———. 1955. Coralsnakes of the genus *Micrurus* in Colombia. Fieldiana, 34:337–359.

———. 1957. The venomous coralsnakes of Trinidad. Fieldiana, 39:55–63.

SCHMIDT, K. P., AND R. F. INGER. 1951. Amphibians and reptiles of the Hopkins-Branner expedition to Brazil. Fieldiana, 31:439–465.

SCHMIDT, K. P., AND F. J. W. SCHMIDT. 1925. New coralsnakes from Peru. Zoological Series of the Field Museum of Natural History, 12:129–131.

SCHMIDT, K. P., AND W. F. WALKER, JR. 1943. Peruvian snakes from the University of Arequipa. Fieldiana, 24:279–296.

SCROCCHI, G. J. 1990. El género *Micrurus* (Serpentes: Elapidae) en la República Argentina. Bolletin del Museo regionale di Sciènze naturale (Torino), 8:343–368.

SHREVE, B. 1953. Notes on the races of *Micrurus frontalis* (Duméril, Duméril and Bibron). Breviora, 16:1–6.

SLOWINSKI, J. B. 1995. A phylogenetic analysis of the New World coralsnakes (Elapidae: *Leptomicrurus*, *Micruroides*, and *Micrurus*) based on allozymic and morphological characters. Journal of Herpetology, 29:325–338.

SMITHE, F. B. 1975. Naturalist's Color Guide. The American Museum of Natural History, New York, New York.

STRUSSMANN, C. AND I. SAZIMA. 1993. The snake assemblage of the Pantanal at Poconé, western Brazil: faunal composition and ecological summary. Studies on Neotropical Fauna and Environment, 28:157–168.

VANZOLINI, P. E. 1986. Levantamento herpetológico da área do estado de Rondônia sob a influência da rodovia. Programa Polonoroeste, Relatório de Pesquisa, 1:1–50.

WAGLER, J. 1824. Serpentum Brasiliensium species novae ou Histoire Naturelle des espèces nouvelles de serpens, recueillies et observées pendant le voyage dans l'intérier du Brésil dans les années 1817, 1818, 1819, 1820 exécuté par ordre de Sa Majesté le Roi de Bavière, publiée par Jean de Spix. Monachii, I–VIII:1–75, 26 pls.

———. 1830. Natürliches System der Amphibien, mit vorangehender Klassification der Säugthiere und Vögel. Ein Beitrag zur vergleichenden Zoologie. J. C. Cotta, München, Stuttgart und Tübingen.

WERNER, F. 1901. Reptilien und Batrachier aus Peru und Bolivien. Abhandlungen und Berichte des Königlichen Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden, 9:1-14.

———. 1927. Neue oder wenig bekannte Schlangen aus dem Wiener naturhistorischen Staatsmuseum (III. Teil). Sitzungsberichte der Akademie der Wissenschaften in Wien. Mathematisch-Naturwissenschaftliche Klasse, 135:243–257.

YANOSKY, A. A., J. R. DIXON, AND C. MERCOLLI. 1993. The herpetofauna of the El Bagual Ecological Reserve (Formosa, Argentina) with comments on its herpetological collection. Bulletin of the Maryland Herpetological Society, 29:160–171.